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Natural History of
BIRDS

1

The Place of Birds in Nature

INTRODUCTION

Birds appeal to a large number of people; some study birds, some watch birds, some merely like birds. The interest may be simple—perhaps only an easy chair before a window facing a feeding station or a bird bath. Yet it may lead to profound research—deep and difficult investigations in the fundamentals of science. It may be professional, though it usually is not (at least among English-speaking people). Interest in birds may entice one person into a nearby woodlot; it may send another into distant lands and remote places. Throughout the whole gamut of bird study, however, runs the thread of kinship interest in birds simply because people like them. No other reason really is needed. Save only for the utilitarian sciences, such as medicine, engineering, or the like, the number of people studying birds and the fund of knowledge consequently built up exceeds that of any other comparable field of science.

The appeal of birds to the intellectual side of man seems to be rather recent. The Stone Age artist who painted a bird on the walls of a cavern or who carved a bird in mastodon ivory is a kindred spirit to the bard whose larks sang at heaven's gate and to the poet whose sandpiper flitted along the beach under sullen clouds that scudded, black and swift, across the sky. For many a generation, birds were left largely to the artist, the poet, and the bard (and of course to the hunter). But with the ascendancy of knowledge over superstition and curiosity over compliance, men of facts and reason moved forward in bird study as in so many other fields. Yet the innate lure to the man of esthetics still supplies much of the stimulation that stirs the man of science. And for this, science may well be thankful.

The Lure of Nature. Though we may be sure that the appeal of nature to man's senses is far from a new discovery, succumbing to it seems clearly more characteristic of today than of any time in the past. The reasons seem associated largely with leisure time and the capacity to get outdoors—along with the means with which to do so. Fundamentally (though man may be too vain to admit it!), the development of cheap ways of substituting mechanical power for human muscle surely is the chief single factor making possible the more extensive study of birds. A people who spend most of their days grubbing for the necessities of life clearly will have few opportunities for indulging in bird study or any other lure of nature. Only directly utilitarian undertakings occur when people must live only to survive.

Scholars debate whether people are interested in natural pursuits because it satisfies some ancient, atavistic hunting instinct inherited from the remote past. Philosophers write of the joy and peace of nature. Yet whatever it may be, the woods and fields and mountains lure more and more people to them each year. Bird life is one of the luring attractions, and bird study shows many signs of continuing to increase in the foreseeable future. Surely, there are no indications that it will decline.

Attractiveness of Bird Study. To those men and women looking for an outlet for their intellectual resources (especially an outlet with an esthetic appeal) when their everyday life fails to stimulate to fullest intellectual capacity or when the stimulation is so great as to generate tension, bird study offers a solid yet relaxing avocation. Birds are living things: they have charm, beauty, and the spirit of life. They may be found nearly everywhere, at all seasons of the year, in all kinds of weather. They may be studied in the neighborhood of the home or in the remoteness of distant places. Bird study may be a solitary pursuit for those who prefer to be alone; it may be group activity for more gregarious spirits. One may study a facet of his own choosing; or he may participate in joint efforts toward a common task (Fig. 1·1).

Whatever may be one's talents, training, or experience in vocational life, often as not it may be applied avocationally to bird study. Birds do about every living thing that man does—whether it be singing, eating, or just getting sick—and some things that modern man cannot—like flying without mechanical contraption, or living permanently and unaided off the countryside. Hence, one studying birds has almost a limitless field before him.

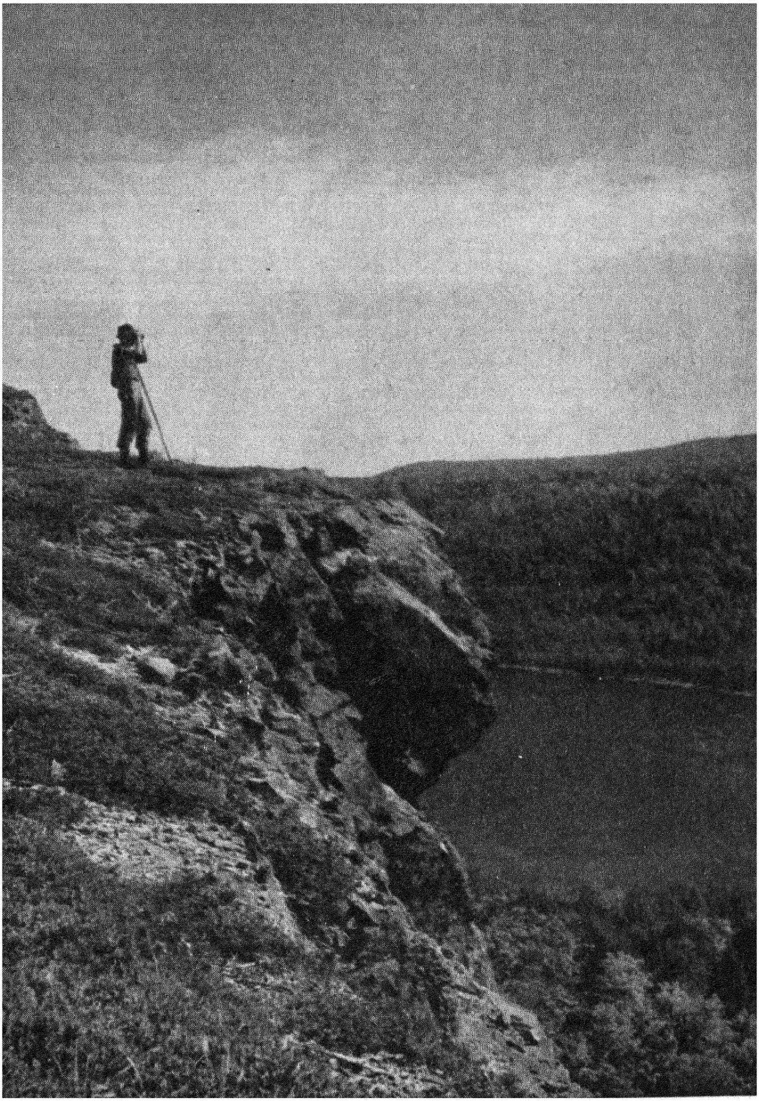

Fig. 1 • 1. *Bird study may be a solitary pursuit for those who prefer to be alone or a group activity for others.*

THE ORIGIN OF BIRDS

The observer of today sees birds that have developed from a long line of continuing evolution, a long series of events in which the steps are unlabeled. The fossil evidence reaching back to Jurassic times, some 150,000,000 years ago (see Geological Time Scale, page 10), indicates clearly that both birds and mammals evolved from reptilian ancestors. The evidence indicates, as one should properly suppose, that modern reptiles have changed less during this period than have mammals and birds.

Many factors operate to obscure our knowledge of the ancestry of birds. There are many gaps in the fossil record. Bird bones are small and delicate and are therefore less likely to be preserved in fossilizing sediments than the heavy bones of other animals. The fact that birds fly makes them less likely to die where their remains might be entombed. We must remember also that birds are largely land forms today and probably were so in the past as well. Obviously, land animals are less likely to be covered by fossil-forming muds than are water animals.

Ancestry of Birds. Fig. 1·2 presents a postulated ancestral line of the bird and indicates the general relationship of birds to mammals and other vertebrates, particularly to the Mesozoic reptiles. Birds are believed to be derived from *thecodonts*, commonly called *ruling reptiles*. The *archosaurs*, the general group to which the ruling reptiles belonged, were derived from *stem reptiles* known as *cotylosaurs*. The cotylosaurs are the earliest known reptilian descendants of the amphibians, which in turn arose from the fish (Fig. 1·3). Mammal-like reptiles as well as turtles seem to have split off from the cotylosaur stem sometime before the rise of the ruling reptiles. The evidence indicates also that lizards and snakes, as well as *Sphenodon*, the curious living reptilian relic of New Zealand, branched off earlier.

The ancestors of the higher archosaurs appear to have adopted a tendency for a bipedal mode of life, and from ancestral archosaurs sprang the dominant reptiles of the Mesozoic. Among these were three specialized groups: the Pterosauria, or flying reptiles; the Ornithischia, or "bird-pelvis" dinosaurs; and the Saurischia, or "reptilian-pelvis" dinosaurs. Sometime during this period, the Crocodilia branched off from the generalized line of ruling reptiles that also gave rise to birds.

It seems most probable that the primitive ancestral birds arose from a generalized archosaur that was somewhat more primitive than Pterosauria, Ornithischia, and Saurischia. It is certain that the bird did not arise from the flying reptiles of the Mesozoic (Fig. 1·4). The

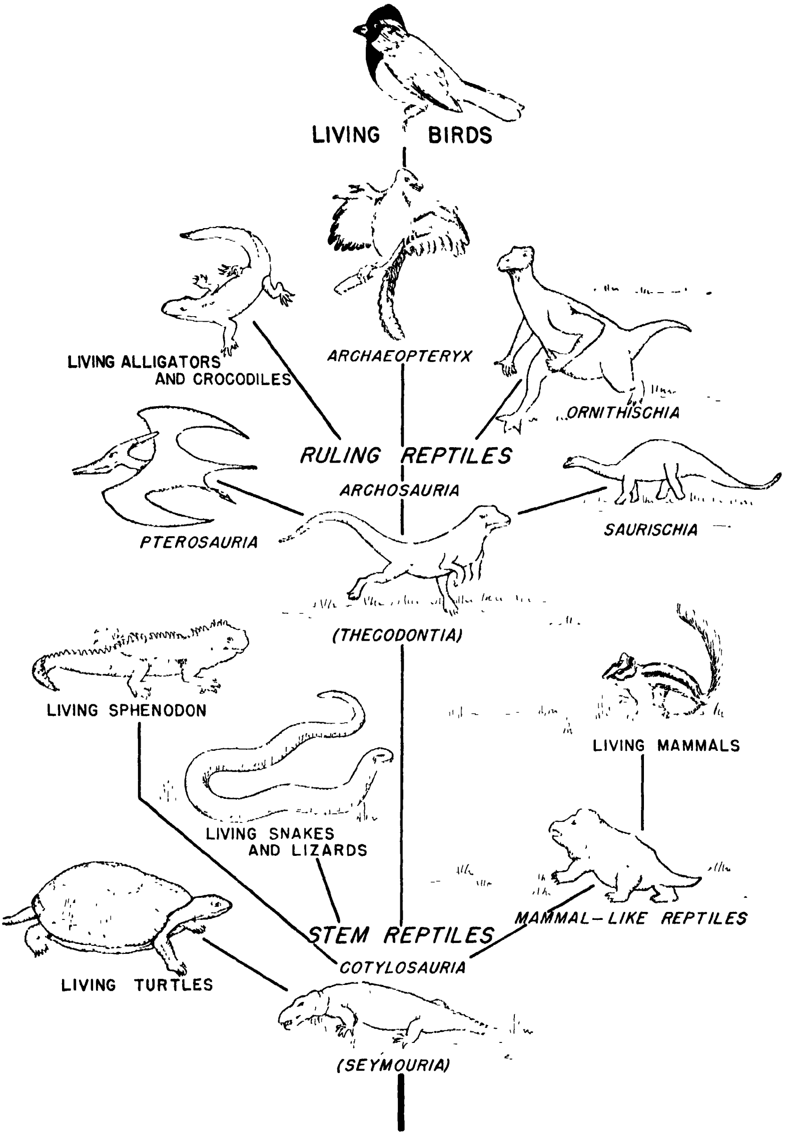

Fig. 1·2. *Postulated ancestry of birds. The thecodont illustrated* (Ornithosuchus) *is generally used to show a primitive ruling reptile, but the common ancestor of birds and later ruling reptiles probably had better-developed forelimbs than those shown. (Prepared by Anne Hinshaw Wing.)*

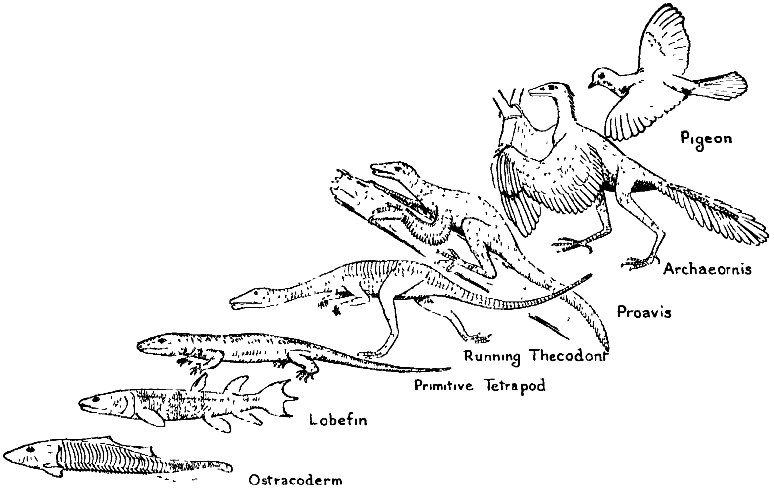

Fig. 1·3. *A suggested evolutionary line of the bird from the fish. (By permission from* Evolution Emerging, *by William K. Gregory, p. 546. Copyright, 1951, The Macmillan Co., New York.)*

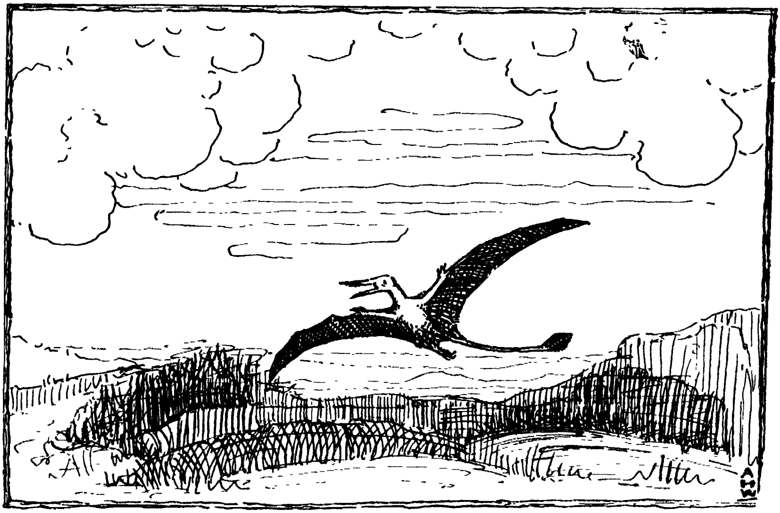

Fig. 1·4. *Restoration of a pterodactyl, a flying Mesozoic reptile not . ancestor of the bird.*

flying reptiles formed a different and most distantly related group. They lived and flew; otherwise, they had little in common with birds. The stem reptiles, from which the ruling reptiles came, probably arose some time in the Paleozoic, perhaps in the Permian. The archosaurs themselves seem to have arisen early in the Mesozoic, during which period the primitive bird line as well as *Sphenodon* may have been initiated.

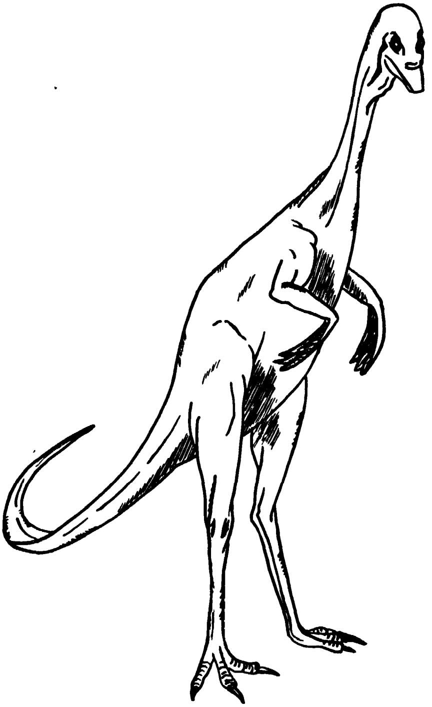

Fig. 1·5. *Restoration of a bipedal dinosaur* (Ornithomimus).

Paleontologists raise some rather fatal objections to the idea that birds came from a bipedal, dinosaur-like Ornithischian (Figs. 1·2, 1·5). One objection is that a bipedal life naturally results in a reduction of the forearm in favor of the hind legs. This can be seen today in the kangaroo, jumping mouse, and many other animals as well as in man himself. If nature abhors a vacuum, it might also be said that evolution dislikes to reverse itself, to backtrack over its trail. If birds developed from a bipedal ancestor, the dwindling forearms would have had to increase in size and importance all over again. Thus evolution would tend to reverse its trend. This objection has been met in part by assuming that the bipedal ancestor lived in the trees (hence, led an arboreal life) and therefore always had well developed forearms.

The similarities of the skeleton are said by some to indicate descent. But more common agreement holds that any similarities might well result from similarities of life or from retention of some ancestral traits not particularly handicapping. Most students of the subject feel confident that, with few exceptions, the more specialized reptiles perished in the upheavals and competitions of the past. Birds thereby arose from a more generalized type of reptile that lived in relative obscurity during the days of dominance by the higher archosaurs.

Mesozoic Birds. Bavarian slate carvers discovered in 1861 the earliest fossil clearly of the bird line, which now goes by the scientific name of *Archaeopteryx macrura*. The slate entombing the fossil belongs to the Upper Jurassic period of the Mesozoic era (see Geologic Time Scale). Although at first paleontologists considered it as possibly a birdlike reptile rather than a true bird, general agreement now con-

Table 1 • 1
Geologic Time Scale

Era	Period and Epoch	Millions of Years Ago to Beginning	Duration (Millions of Years)	Characteristic Events Birds and Other Animals
CENOZOIC Age of Mammals and Birds	Recent			Man, modern birds, and mammals
	(Quarternary)			
	Pleistocene	1	1	Ice age, modern birds. Many birds became extinct.
	(Tertiary)			
	Pliocene	8	7	
	Miocene	20	12	
	Oligocene	35	15	Rise and development of modern birds
	Eocene *	55	20	
MESOZOIC Age of Reptiles	Cretaceous	120	65	*Hesperornis*
	Jurassic	155	35	*Archaeopteryx*
	Triassic	190	35	First mammals
PALEOZOIC Age of Primitive Life	Permian	215	25	Earliest true reptiles
	Carboniferous	300	85	Age of amphibians
	Devonian	350	50	True fishes
	Silurian	390	40	Armored fishes
	Ordovician	480	90	First fishes
	Cambrian	550	70	Invertebrates only
PROTEROZOIC Age of Unicellular Life				Little record of life
ARCHAEOZOIC				

* The early part of the Eocene is sometimes called "Paleocene."

siders it to be a true bird, albeit a reptile-like one. The impressions in the slate beds show that the bird did have feathers; obviously, if it had feathers, it was a bird. A neat point could be made, of course, on when a feather-like structure becomes a true feather, but it seems clear that *Archaeopteryx* possessed true feathers. *Archaeopteryx* was about the size of a Crow, and the skeleton has been well preserved for a bird of this size. Feather impressions of the tail and the wing show plainly; the bones show that the creature had a long tail with feathers sticking out from each side. The completeness of the wing bones also shows a very great advance of evolution; although we may not consider *Archaeopteryx* as a flying bird after the modern manner, it certainly should be considered an aerial one.

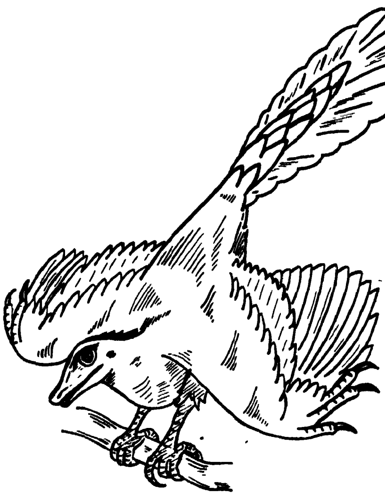

Fig. 1·6. *Restoration of* Archaeopteryx.

Sixteen years later fortune smiled again upon the field of ornithology when in 1877 a second and more complete skeleton of a Mesozoic bird was discovered in the Bavarian slate beds (Upper Jurassic). This bird, about the size of a pigeon, received the name *Archaeornis* (now *Archaeopteryx*) *siemensi* (Fig. 1·6). The feathers on the body show clearly, as do those of the wings and tail. In fact, the feathers are so complete that some even show the presence of barbs, which must have taken a considerable period of evolution for development—and luck for preservation. There can be little doubt but that this creature flew, even though it possessed teeth and other reptilian traits. The sclerotic ring of the eye was as well developed as it is in many contemporary reptiles and in many birds of today (see Fig. 4·20). Thirteen pairs of cone-shaped teeth lined the maxillary and premaxillary bones, where they grew in separate sockets as in reptiles. The ribs of *Archaeornis* (*Achaeopteryx*) lacked the uncinate processes found in modern birds and had a round and slender shape rather than the flattened shape of modern birds. We must not assume from this that uncinate processes were not actually present, for they may have been of cartilage. *Archaeornis* (*Archaeopteryx*) also possessed abdominal ribs, now lacking in birds but still present in reptiles.

A long evolutionary history no doubt lay behind these fossils. The modification of the finger bones for flight certainly must have required a long time, not to mention feather perfection. The substantial humerus, for example, has large ridges for the attachment of flight muscles, and from this alone we may conclude very properly that the wings were rather powerful locomotor organs. The radius and ulna were unmodified for the most part, but the ulna possessed a large head for muscle attachments. The wrist bone and hand bones were present and rather unmodified also, but the finger bones were mostly fused together. The second, or index finger, seems to be like that in modern birds. The third finger was fairly well developed, but the bones of the fourth and fifth fingers had already disappeared. The first finger (thumb or pollex) was but a rudiment even in that early day.

The muscles of the forelimb no doubt had gone through many evolutionary changes. The upper arm muscles apparently were large and powerful, though the hand muscles were almost nonexistent, while those of the lower limbs were much reduced and rather weak as in modern birds. The flight muscles (pectoral) were evidently highly developed and massive in order to operate the arm, a conclusion which has been reached (along with others) through examination of the bony structure.

Cretaceous Birds. During the Cretaceous period lived many kinds of reptiles, on land, in the sea, and in the air. Some of the great flying reptiles had wingspreads of 25 feet (which makes them the largest flying structures before the airplane), and some were small like *Archaeopteryx* and probably even smaller.

In the Cretaceous deposits of Kansas and Colorado occur the remains of a bird that descended to the water and undertook a marine life at the expense of its aerial one. *Hesperornis* lost most of the bones of the wing but had well-developed feet placed far back on the body for strong pushing strokes and surely was a swimmer and diver of superior ability. Teeth still filled the jaws, but in other ways it was clearly avian and shows few primitive characters so evident in earlier forms. A bird fossil described as *Ichthyornis* from the Cretaceous marine deposits of Kansas (on the basis of an incomplete skeleton) has been shown to have had a jaw agreeing with the jaw of mosasaurs. It is concluded therefore that the jaw found with the fossil was not that of a bird (Gregory, 1952).

It seems clear enough, even with the scanty information available through the fossil record, that the bird of the Mesozoic was indeed a bird. Hence, we may conclude that any further development would be more properly the evolution of the bird rather than its origin. The study of birds from the Mesozoic onward becomes the study of creatures already birds. The birds of the Mesozoic may therefore be considered as true birds but with strong reptilian leanings; those of the Cenozoic were essentially modern birds.

BIRD RELATIONSHIPS

Because birds are animals, they must be examined and considered with respect to other animals (though by themselves they form a well-marked group, which often enough is sufficiently satisfying to students of ornithology). Their relatives are more than just the reptiles from which their line came so long ago in human concept but so recently in the light of geological time.

Biologists recognize two major divisions of living things and have designated them as the PLANT KINGDOM and the ANIMAL KINGDOM.* While it is simple to classify common organisms as either plants or animals, such simplicity fails in border-line cases. In a sense, this should not be surprising, for there is no reason to believe other than that all life evolved from the same source and that a division—however indistinct—occurred somewhere along the line.

Phylum. The living things of the ANIMAL KINGDOM have been divided into a number of great groups, called phyla, having distinct enough characteristics so as to indicate affinity. Zoologists do not always agree upon the characteristics that indicate relationships. Nor do they always agree upon what are or are not phyla. In order that birds may be visualized in proper perspective and in order that bird students who are not familiar with the various phyla may have their names available for ready reference, the twenty-one of more general agreement are given below:

PROTOZOA	(Animals of one cell)
MESOZOA	(Parasitic, primitive multicell animals)
PORIFERA	(Sponges and their allies)

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* Some biologists consider Fungi to be a third kingdom. Some also have doubts about the classification of bacteria, rickettsia, and viruses in the scheme of two kingdoms.

Coelenterata	(Radial animals with nematocysts; polyps and medusas)
Ctenophora	(Radial animals without nematocysts; comb jellyfishes)
Platyhelminthes	(Flatworms)
Nemertinea	(Nemertine or freshwater flatworms)
Entoprocta	(Minute stalked animals)
Aschelminthes	(Round and horsehair worms)
Acanthocephala	(Thorn-headed worms)
Bryozoa	(Colonial, aquatic organisms)
Phoronidea	(Wormlike, marine animals)
Brachiopoda	(Marine, shelled animals)
Echinodermata	(Radially symmetrical animals)
Chaetognatha	(Small, aquatic worms)
Mollusca	(Oysters, clams, and their allies)
Annelida	(Segmented worms)
Sipunculoidea	(Peanut worms)
Priapuloidea	(Marine organisms)
Echiuroidea	(Marine organisms)
Arthropoda	(Jointed-limb animals with exoskeltons)
Chordata	(Animals wtih a notochord)

Chordata. Birds belong to the phylum Chordata, which may be separated into several subphyla and classes:

Phylum Chordata
- Subphylum Hemichordata.* (Marine, wormlike chordates with gill slits)
- Subphylum Tunicata. (Marine, larva-like animals covered with a "tunic")
- Subphylum Cephalochordata. (Small fishlike primitive chordates)
- Subphylum Agnatha.** (Vertebrates without jaws and usually without paired fins or appendages)
  - Class Cyclostomata (Lampreys and hag-fishes)
- Subphylum Gnathostomata.** (Vertebrates with true jaws and usually with paired appendages)
  - Class Chondrichthyes (Sharks and rays)
  - Class Osteichthyes (Bony fishes)
  - Class Amphibia (Amphibians)
  - Class Reptilia (Reptiles)
  - Class Aves (Birds)
  - Class Mammalia (Mammals)

Characteristics of the Bird. All chordates have a *notochord*. It appears briefly in the embryo, but serves no longer as a stiffening rod in the adult, as it does in amphioxus and in cyclostomes. It does serve however, as the foundation around which the bird backbone forms during embryonic development. Chordates all have pharyngeal gill slits. They are present in the early bird embryo but develop into other structures as the bird grows. All chordates have a nervous sys-

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* Some zoologists call this a phylum.

** Many zoologists prefer to use the single subphylum Vertebrata for these; others prefer to use Craniata.

tem *dorsal to the digestive tract*, a characteristic seen in any bird dissection (Fig. 1·7). The bird has a *vertebral column* as well as a cranium. We can readily understand why the bird is placed in the Subphylum Vertebrata or Subphylum Craniata, as the choice may be. Birds also show the vertebrate or chordate characters of *bilateral symmetry*, *internal metamerism* (segmentation), *anterior mouth*, and division of the body into *head*, *trunk*, *tail*, and *limbs*.

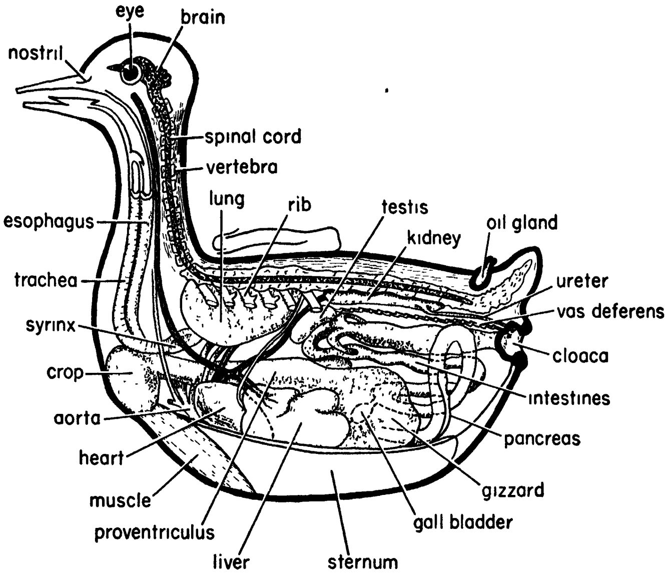


Fig. 1·7. *Internal anatomy of the Domestic Chicken shows the general character of the bird anatomy.*

All classes of vertebrates have characters that are designated as *distinguishing characteristics.* Not always are these the exclusive possession of one class but may be shared with one or more others. The nine most commonly used distinguishing characteristics for birds (class AVES) may be listed as follows:

1. Possess feathers
2. Primarily land dwellers
3. Possess four limbs
4. Adapted for aerial life
5. Homoiothermous (warm bloodedness)
6. Have four-chambered heart
7. Right aorta only usually persists
8. One occipital condyle
9. Lay eggs and care for young

All birds, even the most aquatic of Grebes, Penguins, and Albatrosses, return to land (or shore) for nesting. The aquatic adaptation of such birds is secondary, however, for they must return to land during the breeding season.

The bird shares a bipedal mode of life with the extinct *ruling reptiles* (as well as with a few scattered animals, including man). The ruling reptiles too had four toes to the foot (and some had three

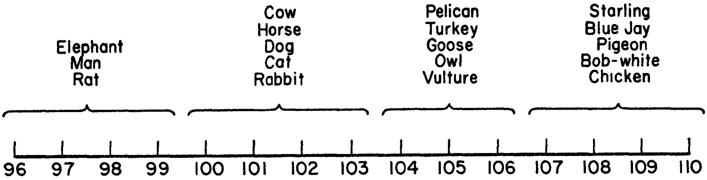


Fig. 1·8. *The body temperature of birds varies from about 104° F. to about 110° F., somewhat higher than in mammals.*

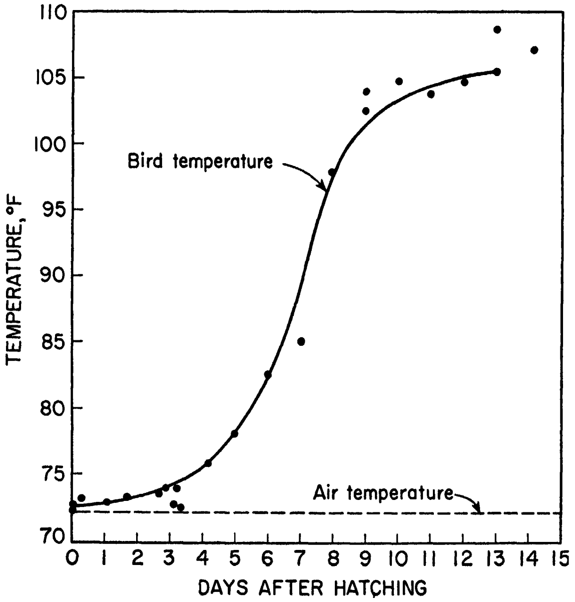


Fig. 1·9. *The newly hatched bird has little temperature control and is essentially "cold-blooded." Body temperature becomes established for the House Wren on about the ninth day. (Modified by Kendeigh from S. Charles Kendeigh and S. Prentiss Baldwin,* Physiology of the Temperature of Birds, *Cleveland Museum of Natural History, Science Publications, No. 3, 1932.)*

fingers on the forelimb, also in common with birds). The bare essential bracing of any structure is four ways. The bird therefore has two toes set at an angle for side sway, one ahead for forward tip and usually one behind for rearward tip. To facilitate walking, the side "braces" have moved forward somewhat. The rear toe has diminished in importance in some walking (but not perching) birds.

Warm bloodedness (*homoiothermous*, technically, constant temperature) birds and mammals have in common. Other vertebrates are cold blooded (poikilothermous), and their body temperature varies with that of the surrounding medium rather than being almost wholly independent as in homoiothermous animals. The temperature of placental mammals normally ranges between about 96° F. and 103° F., according to species, while that of birds ranges between 104° F. and 110° F. (Figs. 1·8, 1·9). In a sense, mammals are warm-blooded and birds are "hot-blooded," but the temperature of a hibernating mammal may reach about 36° F. and that of a torpid Nighthawk drop to 80° F. In summer a reptile may have a temperature matching that of the air,

Table 1·2

Comparative Class Characters

Reptiles	Birds	Mammals
Four limbs	Four limbs (front limbs modified)	Four limbs
Dry skin	Dry skin	Dry skin
Scales	Feathers	Hair
Two aortas present	Right aorta only usually persists	Left aorta persists
Poikilothermous	Homoiothermous	Homoiothermous
Nucleated ovoid corpuscles	Nucleated ovoid corpuscles	Nonnucleated discoid corpuscles
One occipital condyle	One occipital condyle	Two occipital condyles
Sac-like lungs	Fixed lungs	Elastic lungs
Three-chambered heart (or incompletely four-chambered *)	Four-chambered heart	Four-chambered heart
Egg laying	Egg laying	Young born alive (usually)
Seldom care for young	Care for young	Care for young
Two ovaries functional	Right ovary degenerate	Two ovaries functional
Rudimentary corpus callosum	Small corpus callosum	Well-developed corpus callosum
Poorly developed cerebellum	Well-developed cerebellum	Well-developed cerebellum
	Oblique septum	Diaphragm
		Mammary glands

* The Crocodilia have a four-chambered heart, but a slight mixing of blood may occur, so that they should be considered as lacking the completeness of four chambers as in birds.

which may exceed 100° F. Prolonged exposure to a temperature much above 112° F., however, may be fatal both to reptiles and to birds.

Reptiles, Birds, and Mammals Compared. The long time that has separated the reptiles, birds, and mammals from each other has made for many differences. Yet many things in common have been retained. A comparison of some characteristics of the three groups indicates the relationships of several of the comparative characters (Table 1·2).

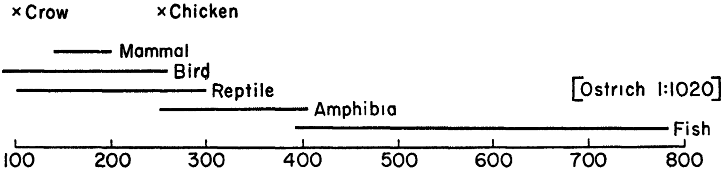


Fig. 1 · 10. *Ratio of heart size to body size in vertebrates. Heart-body ratios of birds are indicated by X. (The ratio of heart size to body size in the Ostrich is of too great a magnitude to be shown in this figure.)*

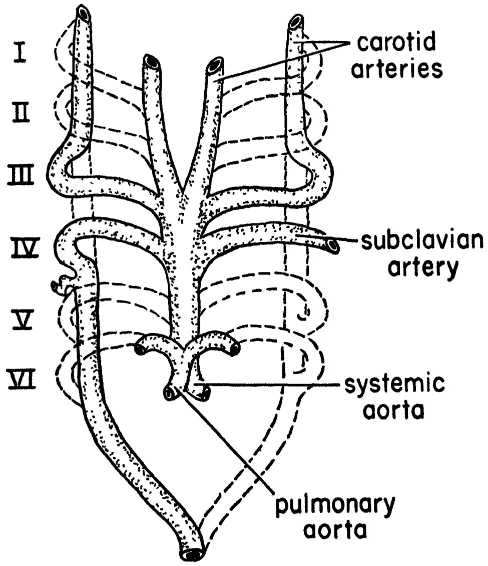


Fig. 1 · 11. *The right aortic arch is the one that usually remains in the adult bird (and the left in the adult mammal) though the reptile has both functional.*

The greatly modified wings of today seem unique. They have three digits remaining, but reduction in the number of digits to three occurred among the ancient reptiles. The hollow bones of birds are likewise unique among living animals, though some extinct reptiles had them. Sclerotic plates, which strengthen the eye in birds, have been found in some reptiles; the fossil remains of Mesozoic ichthyosaurs and pterosaurs show them.

The four-chambered heart of the bird is comparable to that of the mammal and is of about the same or greater proportionate size (Fig. 1·10). Usually little or no trace of the left aortic arch remains in the adult bird (Fig. 1·11).

Replacement of teeth with a horny beak characterizes modern birds, but extinct birds had teeth and modern turtles have beaks. At the opposite end of the body, the tail has been much reduced. No reptile and few mammals have so great a reduction. The hind limb of the bird has an *intratarsal* or *mesotarsal* joint in common with some reptiles (page 57). Even the outer surface of the lower leg and foot of the bird still bears scales, which is probably an ancient reptilian trait still efficient in protecting the foot with a light-weight covering (Fig. 1·12).

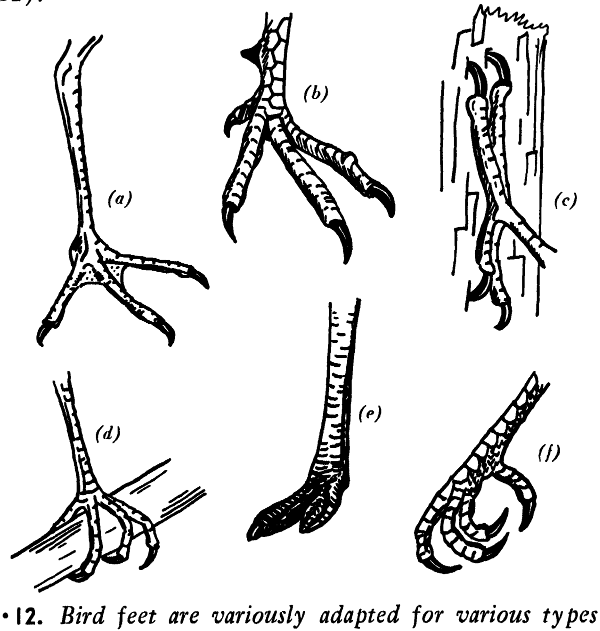


Fig. 1·12. *Bird feet are variously adapted for various types of life. (a) Yellow-legs, (b) Pheasant, (c) Flicker, (d) Passerine, (e) Ostrich, (f) Hawk.*

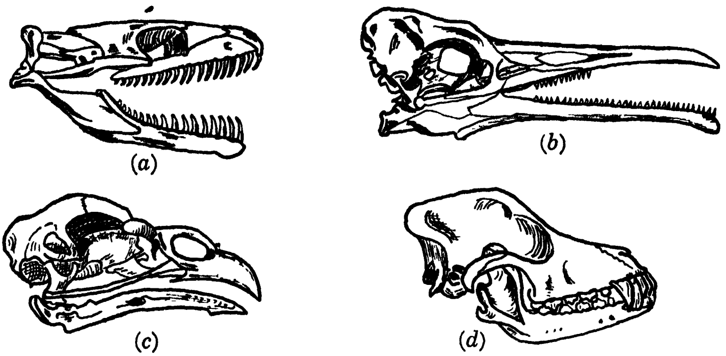


Fig. 1 · 13. *Skulls of* (*a*) *modern reptile,* (*b*) *ancient toothed bird,* (*c*) *modern bird, and* (d) *modern mammal.*

The skull shows many special variations distinctly unlike those of any reptile, but the skull also shows many retentions of reptilian form. The several bones forming the lower jaw are rather similar to those of reptiles (Fig. 1·13), though even in early birds, the jaw seems to have differed. There have been marked changes in the brain, especially in the increase of the cerebrum and cerebellum (Fig. 4·18).

Adaptations for Flight. The use of flight, the most outstanding single controlling characteristic of birds, dominates the whole nature of the creature. As in an airplane, the framework plays a leading role. But the framework of the terrestrial ancestor, whatever it may have been, has had to be drastically adjusted to fit it for flight.

Because all soft parts are fastened to the skeleton, the bony framework forms a good place for beginning a general discussion of flight adjustments. The entire skeleton has become compact; much of this has been brought about by fusion of parts, particularly of the bony basket itself, and consequent reduction in bulk through elimination of connective tissue, ligaments, muscle, and other soft parts. Fusion makes for rigidity; in consequence, the bird body itself has little movement. Reduction of weight in proportion to motive power increases flight capacity, and birds carrying less "dead weight" have a distinct flying advantage over others. Increase in use of hollow bones and shifting of weight from extremities accompany marked flight improvement. This is especially true in respect to the wings and legs that have to be swung in an arc like a pendulum, or otherwise moved when suspended (Fig. 1·14).

Allied with skeletal compactness is the general streamlined shape of the body. Full streamlining requires a blunt forward end tapering to a pointed stern. The faster flyers are much better streamlined than

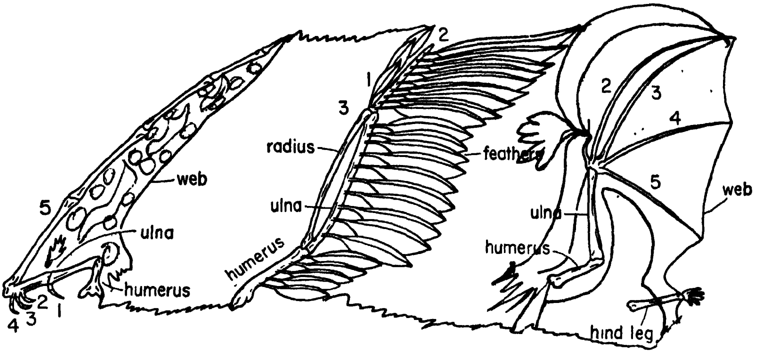


Fig. 1 • 14. *Comparison of the wings of a flying reptile, bird, and bat. The numbers indicate which digits are present in the wings.*

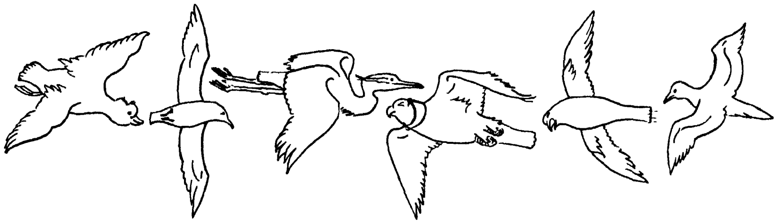


Fig. 1 • 15. *Varying degrees of streamlining in birds. Left to right: Duck, Shearwater, Heron, Falcon, Swift, Booby.*

the slower ones (Fig. 1·15). The Chimney Swifts show this especially well; they have a short, rather large and blunt head. The feathers of the neck carry the streamlining into the shoulders and breast, the greatest circumference of the body. From the shoulders rearward, the body tapers to a short tail. Even the feet have been reduced in size and strength, and the pelvic girdle along with them, so that the feet fit into the streamlined feather mass when drawn up. In line with this reduction in foot power, the Chimney Swift can cling well only on vertical surfaces where its tail can help the weak feet.

The penetration of so many parts of the body by air sacs seems to help somewhat in flight efficiency. But air sacs function chiefly for cooling. Air uses less weight to carry heat from the interior than does blood. The heat is expelled directly to the exterior rather than indirectly by conduction, radiation, or evaporation. In a sense, the bird has an "air-cooled" body in marked contrast to the "liquid-cooled" body of man.

Another trend in the bird world, again in line with aerial life, is the movement of weight to the interior, so that the center of gravity tends to lie slightly back of the wings. The shift in emphasis from muscles in the wings to the great pectoral flight muscles in the body exemplifies this (see Fig. 4·2). The wing is *raised* by the inner breast muscles *below* the wings rather than by topheavy back muscles. The heavy teeth of other vertebrates have been replaced by a light, horny beak. The grinding function has been taken over in those species needing it by a muscular gizzard. The weight of the gizzard may be no less and perhaps actually greater than some jaw muscles, bones, and teeth for mastication. But the additional neck structure needed to support a heavy chewing jaw is not needed, and thus the gizzard setup probably weighs no more than a jaw and its accessories. But it is in the middle of the body instead of at the end of a column. The reduction in head weight has been paralleled by loss of the heavy reptilian tail, which if persisting would require counterbalancing by shifting weight forward of the wings or shifting the wings backward.

The intestines, especially the large intestines, have also been reduced in bulk. In fact, the entire internal organs evidently have been abbreviated when possible to do so without materially lowering physiological efficiency. It is likely that one of the functions of the high body temperature of the bird may be to increase energy output with reduction of weight.

The inability of the bird to use the forelimbs as arms and hands would be a handicap in feeding, nest construction, and the like were it not that a flexible neck has evolved to make it possible for the beak to take over such tasks as are usually performed by "hands." The development of a flexible neck releases the forelimbs for flying and puts the forceps that take up food at the front, along with the mouth.

We can safely make the general statement that the skeletal structure of the bird uses practically all the sound engineering principles for combining strength, rigidity, and economy of material. Among these may be listed:

T-beam construction of sternum (primarily for muscle attachment)
I-beam construction in many bones
Tubular bones
Flattening and overlapping of rib processes for shaping and bracing
Fusion of parts, like castings
Fusion, thinning, ossification of brain case for lightness with strength

Distinguishing Features of the Bird. A summary of the important factors and adjustments that distinguish the bird from other animals or mark its "high-speed" way of life would include:

An insulating layer of feathers
Primary adaptation for land life
Absence of skin glands except uropygial or wattle glands

Forelimbs modified into wings with three digits (Fig. 1·14; some ancient reptiles had three digits)
Homoiothermous (as are mammals)
High body temperature
Four-chambered heart (as also in Crocodilia and mammals)
Large heart (proportionately the largest of any organism)
Large blood vessels (proportionately the largest capacity of any organism)
Single, right aorta
Lung air sacs (in unrelated chameleons also)
Excurrent and incurrent bronchi
Hollow bones (Some unrelated pterodactyls had them.)
Metanephric kidney (in reptiles and mammals also)
No urinary bladder
Single left ovary and oviduct (Some Hawks may have two ovaries nearly equally developed.)
Uncinate processes on ribs (found in the reptilian *Sphenodon* also)
Eyes highly specialized (perhaps no more than many other animals)
Greatly elongated, *tetraradiate* pelvis (as in some reptiles)
Hind limb with intratarsal joint (as in some reptiles)
Extensive fusion of trunk vertebrae
Fusion of vertebrae with pectoral girdle
Greatly reduced tail
Lack of teeth which are replaced by horny beak (Some extinct birds had teeth and modern turtle has a beak.)
Egg laying (as in reptiles and mammalian Prototheria)
Eggs incubated by heat of body (but egg and embryonic membranes essentially reptilian)
Parental care of young highly developed
Scales on lower legs and feet
Diapsid skull (as in most reptiles)
Prelachrymal fossae (as in some reptiles)
Cloaca present
Several bones of lower jaw as in reptiles
Single occipital condyle present
Bipedal (as in some reptiles and as in man)
Four limbs (as in amphibians, reptiles, and mammals)
Adapted for aerial life
Communication by sound and song

SUGGESTED READING

GREGORY, WILLIAM K., *Evolution Emerging.* New York: The Macmillan Co., 1951.
HEILMANN, GERHARD, *The Origin of Birds.* New York: Appleton-Century-Crofts., Inc., 1927.
HYMAN, LIBBIE HENRIETTA, *Comparative Vertebrate Anatomy.* Chicago: University of Chicago Press, 1942.
NEWMAN, H. H., *The Phylum Chordata.* New York: The Macmillan Co., 1939.
*ROMER, A. S., *The Vertebrate Body.* Philadelphia: W. B. Saunders Co., 1950.
*STORER, TRACY I., *General Zoology.* New York: McGraw-Hill Book Co., Inc., 1951.
*YOUNG, J. Z., *The Life of Vertebrates.* Oxford: Clarendon Press, 1950.

* Books especially useful or interesting to people interested in birds are designated by an asterisk (*).

2

Classification and Nomenclature

The mind of man cannot embrace the vast array of separate items of knowledge available to it. Naming and arranging objects is a fundamental human trait, not just an invention of naturalists. Primitive man thousands of years ago doubtless named things and grouped like ones together in his mind, which thus made for him a crude system of classification and nomenclature. But no matter how crude, classification and nomenclature are systems of organization. The brain can comprehend and remember an amazing mass of information that has been systematically arranged.

THE ELEMENTS OF TAXONOMY

In the science of classification, similar animals (or plants in the PLANT KINGDOM) are arranged together into related groups. But before they can be so arranged, their relationships to each other and to other groups must be determined. In addition to being given a name, their salient characters must be listed so that another may recognize and identify them. Sorting (*classification*), naming (*nomenclature*), and describing (*description*) together constitute classical *taxonomy*. But the very great accumulation of information on the biology of living birds has brought about a marked change of emphasis in bird taxonomy. While earlier it concerned itself chiefly with the study of relationships as shown by bird skins and anatomy, some taxonomists now recognize that any bird characteristic, whether of behavior, physiology, ecology, or structure, may show relationships. Hence, some more advanced taxonomy may more correctly be considered as having become comparative bird biology in a synthesis of all ornithological knowledge around the theme of relationship. In a somewhat similar way, this book is one of comparative bird biology, but its theme is the life of the living bird.

Relationship. The fundamentals of relationship among birds are similar to those in man's own family connections—i.e., siblings are more closely related than first cousins. The determinant is *distance removed from the common ancestor.* Thus siblings are one step removed, first cousins are two steps removed, and so on. In actual practice, the taxonomist may judge relationship only on the basis of the birds as they are today. The connecting links have long since disappeared, and the continuous record has been broken except as we are able to determine it directly from fossils (Fig. 2·1) and indirectly from modern or recent birds and their attributes. *Morphological characters* are used to indicate major relationships, although other characters may be used as supporting evidence. The more like the ancient, fossil ones a living bird is, the more *primitive* it is said to be. In addition to the evolved character of the bird itself (Chapter 9), among the many things that may indicate relationship are such things as parasites; evidently parasites stayed with their host through its evolutionary history and may show relationships not readily apparent in the bird itself (page 405).

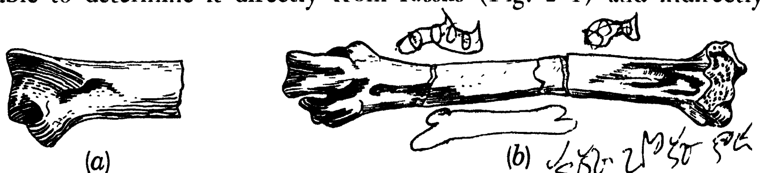


Fig. 2 • 1. *Exhaustive study of fossil remains tells paleontologists something about the bird. Comparison of the skeletal structure of the fossil with known birds gives additional ideas about the probable life of the ancient bird.* (*a*) *Distal end of ulna of* Palaeoborus rosatus *of the Miocene, related to Old World Vultures.* (*b*) *Tarsometatarsus of* Paranyroca magna *from the Miocene, a distant and primitive relative of the Anatidae about the size of a Swan. These are type specimens.* (*After Alden H. Miller and Lawrence V. Compton, "Two Fossil Birds from the Lower Miocene of South Dakota,"* Condor, *41(1939):155*).

Species. The smallest major unit recognized by avian taxonomists is the *species* (though there may be subunits within a species). While we cannot set up any criterion for a species so definitive as to leave no room for doubt, it does seem possible to have a practical definition. *A species may be defined as a population of animals that breed freely* *among themselves but are reproductively isolated from others.* Thus the Crow of North America is a species. The Raven that looks just as black is a different species, for Ravens and Crows do not cross in nature. They are *reproductively isolated,* but the exact mechanism for this is immaterial to our recognition of the fact of isolation. A familiar example or two may clarify this concept further.

The Downy and Hairy Woodpeckers of North America bear striking resemblances to each other. The color pattern of one, for example, duplicates that of the other except for a few minor differences, as in the presence or absence of bars on the tail. There can be little room for doubt that these two species are closely related to each other. Yet no case has been found where these two birds clearly cross, even though they occupy much the same range over the continent. To such birds has been applied the term *sympatric species* (see also *allopatric* species, Chapter 10).

The Peregrine Falcon inhabits much of the Northern Hemisphere, both Old World and New World, wherever conditions are suitable for it. The Falcons of America are geographically separated by water from those of the Old World; yet the birds are the same, for they grade completely into each other from one end of the range to the other. But in western America, the Prairie Falcon differs somewhat from the Peregrine and no interbreeding occurs between them. The Pergerine and Prairie Falcons are thus reproductively isolated, even though not now geographically isolated. Hence, they constitute two different though closely related species.

Subspecies. Birds of wide distribution and some of rather restricted distribution sometimes break up into geographic groups called *subspecies.* These may be referred to sometimes also as *races* or *forms.* In a sense, subspecies mark the plasticity of a species in adapting itself to ecological conditions. But the life habits and characteristics of the species affect this plasticity. A resident species, for example, tends to have more subspecies than a migratory one. The Canada Jay illustrates well the break-up of a wide-ranging species (nearly 2,500,000 square miles) into many races (Fig. 2·2). The ten subspecies illustrated inhabit separate ranges having areas of about the following square miles:

fumifrons	1,002,400	*obscurus*	67,200
pacificus	12,320	*griseus*	117,600
albescens	851,200	*connexus*	128,800
canadensis	815,000	*bicolor*	156,800
rathbuni	8,000	*capitalis*	274,400

Genus. When one looks at the various species with which he is familiar, he notes that several sometimes resemble each other more

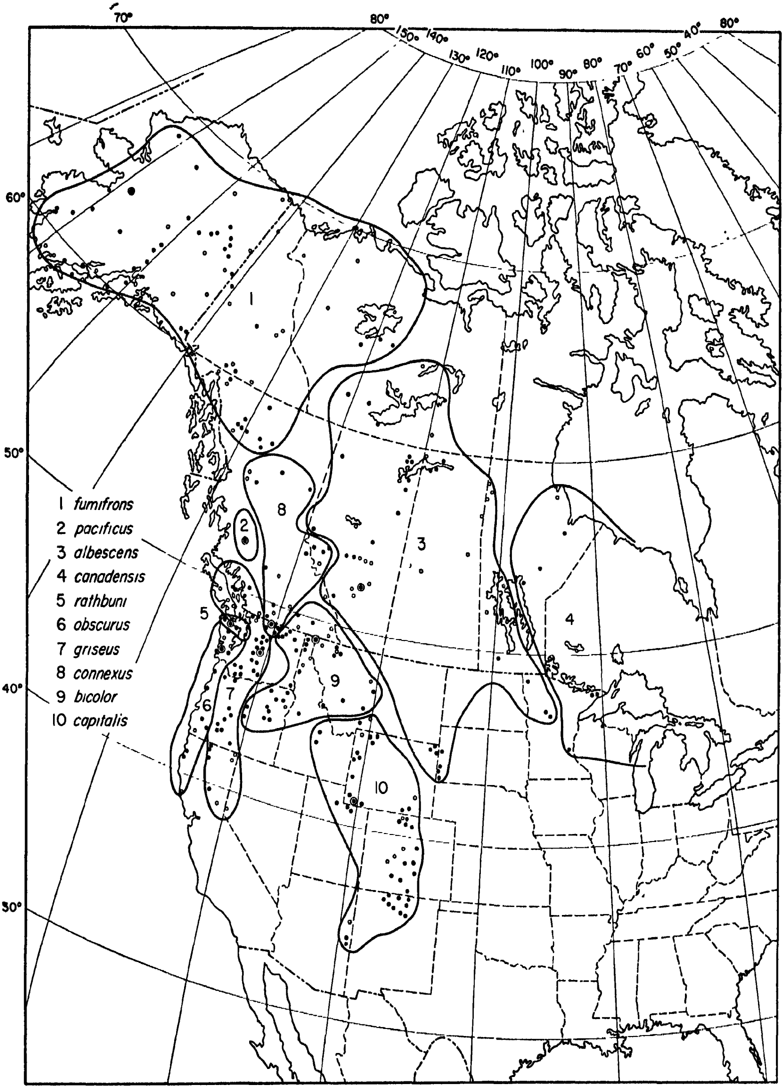


Fig. 2·2. *Distribution of western races of the Canada Jay* (Perisoreus canadensis). *Solid dots show localities of one or more specimens examined by the taxonomist in reviewing the status of the subspecies. Circles represent other records of occurrence and dots enclosed by circles locate type localities. (From John W. Aldrich, "Relationships of the Canada Jays in the Northwest,"* Wilson Bulletin, *56(1943):220.)*

than they do others. Anyone familiar with the Lincoln, Swamp, Fox, and Song Sparrows of America should be able to see that they resemble each other more than they do other native Sparrows. Taxonomists place such groups of species in divisions, each known as a *genus* (plural *genera*). A genus, therefore, is made up of a number of closely related species. The characters commonly used by avian taxonomists in forming a genus are generally plumage pattern and bill shape.

Family. Many genera in turn bear resemblances to each other that set them apart from other genera. Families are formed of such groups of genera. The characters ordinarily used to group genera into families are often bone structure, bill shape, wing formula, and tarsal scales, but they may include additional characters.

Almost everyone recognizes the gallinaceous, chicken-like birds as being related to each other. Taxonomists have divided these birds into several score of genera. Among the gallinaceous birds will be found several groups of genera that look and act much alike, and seem more closely related among themselves than to other groups. One such group of eleven genera bears the mutual common name of "Grouse" in recognition of this similarity. They belong to the family Tetraonidae. Other American gallinaceous relatives of Grouse belong to Meleagrididae (Turkey), Phasianidae (Pheasants, Quails), and Cracidae (Chachalaca, Curassows, Guans). The characters that separate the Grouse from the other groups are their mutual similarity of habits, appearance, and structure. They are the only gallinaceous birds, for example, that have feathered nostrils and feathered tarsi. All of them also develop "snowshoes" in winter; their distribution is boreal. It is clear that the Grouse descended from a common, Grouse-like ancestor, just as all Phasianidae came from some other ancestor of Pheasant-like habits. It is quite likely, however, that Tetraonidae, Phasianidae, and other gallinaceous families long ago had a common ancestor.

Order and Class. Various families of birds show mutual similarities, and they in turn are grouped into *orders*, the largest taxonomic group within the *class*. Thus, all gallinaceous birds, regardless of family, belong in the order *Galliformes*. All Hawks, Falcons, and their allies belong in the order *Falconiformes*. Thirty-four such orders are currently recognized today; this includes known fossil orders. (We have no idea, of course, how many extinct ones there are.) The chief characters used in establishing these orders are the shape and proportions of the bones.

The Ruffed Grouse of the northern forests is classified as follows:

Kingdom: Animal
  Phylum: Chordata

Subphylum: Vertebrata
  Class: Aves
    Order: Galliformes
      Family: Tetraonidae (Grouse and Ptarmigan)
        Genus: *Bonasa*
          Species: *umbellus*

Although the eight groupings shown in the example are the standard ones in animal taxonomy, additional ones are often used for convenience. A family having a large number of genera may have several genera resembling each other more than they resemble the remaining genera. The family may thus be divided into *subfamilies.* Additional groupings may include:

Subclass
Superorder
Suborder
Superfamily
Subfamily
Subgenus
Subspecies

SCIENTIFIC NOMENCLATURE

Scientists have used the Latin and Greek languages for scientific names (Latinized) because the grammar and forms of a "dead" language are static and therefore do not change as modern languages do. The names of the various orders, families, and other classifications of birds have been more or less standardized by the International Rules of Zoological Nomenclature. The names of the orders, for example, end in *-iformes* (e.g., Galliformes), although some ornithologists still use older names which were compiled before an attempt was made to bring about more uniformity in scientific nomenclature. The names of families end in *-idae* (e.g., Tetraonidae) and those designating subclass end in *-ornithes.* In addition, the following endings are used for other groupings: *-gnathae* for superorder, *-oidea* for superfamily, *-i* or *-ae* for suborder, and *-inae* for subfamily. The use of the various endings can be illustrated by the complete classification of the Desert American Sparrow Falcon in groups, subgroups, and supergroups, from class to subspecies:

Class: Aves (Birds)
  Subclass: Neornithes (True Birds)
    Superorder: Neognathae (Typical Birds)
      Order: Falconiformes (Vultures, Hawks, and Falcons)
        Suborder: Falcones (Hawks, Falcons, and Secretary Birds)
          Superfamily: Falconoidea (Hawks and Falcons)
            Family: Falconidae (Falcons and Caracaras)
              Subfamily: Falconinae (Falcons)
                Genus: *Falco* (Falcons)
                  Subgenus: *Cerchneis* (Kestrel Falcons)

Species: *sparverius* (American Sparrow Falcon)
  Subspecies: *phalaena* (Desert American Sparrow Falcon)

The name of the bird for taxonomic reference is *Falco sparverius* Linnaeus (but for nontaxonomic use, the English name American Sparrow Falcon would be used; the taxonomic reference name may be added for possible clarification). This name is called a *binomial name* and the system of nomenclature by which it gets this name, the *binomial system*. In the example given, *Falco* is the generic name (and is always capitalized), *sparverius* is the species name (and is never capitalized), and Linnaeus is the man who so named it (in other words, the *describer* or *authority*). The bird of the Southwest was described separately and carries the subspecies name of *phalaena*. The authority for this name was Lesson, who described the bird originally as *Tinnunculus phalaena*. When transferred to the genus *Falco*, the name *phalaena* continues as the species or subspecies name, as the case may be. The name of the authority is then placed in parenthesis to indicate the change of genus. The complete citation for the Desert American Sparrow Falcon thus becomes *Falco sparverius phalaena* (Lesson).

The Work of Linnaeus. The binomial system of classification now used by taxonomists for birds comes from the work of Karl von Linné (1707–1778), a Swedish naturalist (known better by his Latinized name of Linnaeus). While he was chiefly a botanist, the application of his classification system to zoology is pre-eminent. Its suitableness to animals was rather soon apparent, and the basic system became universally recognized and used by zoologists. It has, of course, been much modified and amended since the time of Linnaeus. Over the years, animal taxonomists have come to agree upon the Tenth Edition of *Systema Naturae* by Linnaeus (1758) as the starting point for classification and nomenclature. This book listed 4,236 animals of all kinds, among which were 564 species of birds, about 15 per cent of the number known today.

Rules of Nomenclature. It is obvious that in the development of any body of knowledge, certain procedures should develop and become traditional. In the case of taxonomy, these have become established as working *codes* by several recognized organizations. Among these are the *American Ornithologists' Union Code* and the *International Rules of Zoological Nomenclature*. The latter code, adopted by the Fourth International Zoological Congress at Berlin in 1901, sets forth among others the following dictums:

Zoological names are independent of botanical names.
Species names are binomial (subspecies names are trinomial).

Scientific names are Latin or Latinized words.

The original spelling is preserved unless a typographical error has occurred.

The name of the authority (the first person to publish a name with a recognizable description) follows the scientific name (enclosed in parentheses if the species is later transferred to another genus).

The first name published in accord with the rules (including a recognizable description) has priority over others.

Linnaeus' *Systema Naturae*, Tenth Edition (1758), is the starting point for scientific names.

The International Commission of Zoological Nomenclature acts as a sort of "supreme court." Questions arising under the rules and appearing to need formal determination are transmitted to the commission through a laborious procedure provided by the rules. Zoologists usually accept opinions adopted by the Commission as final.

Check Lists. Several *check lists* and *species catalogs* of birds have appeared from time to time giving names accepted by the author or body preparing the check list or catalog.(A catalog differs from a check list by giving descriptions and often more detailed citations of other names that have been used for the same species.)In North America a committee of the American Ornithologists' Union has from time to time prepared check lists and supplements which give the scientific names of birds agreed upon as acceptable by the committee on behalf of the society. The check list also gives a summary of ranges, both breeding and winter. In general, American bird students follow most of the check list scientific names, though the designated common names have not been so widely accepted.

The most widely accepted, authoritative world-wide check list is the *Check-List of Birds of the World* (Peters, 1934—). It gives ranges in general terms and, like most check lists of its type, gives citations to the original description. The monumental work, *Birds of the Americas* (Cory and Hellmayr, 1918—), has special usefulness, though it is a catalog rather than a check list. The British Museum *Catalogue* (Sharpe, 1874–1898) and *Hand-List* (Sharpe, 1909–1912) are also of value. Because most ornithologists are not classical scholars, works like Coues' *Check-List* (1882) or *Key* (1927) are especially useful in giving origins and meanings of scientific names of American birds.

Taxonomic Practice. Naming a bird necessitates that the new name be accompanied by as complete a description as possible, with considerably more detail than that found in descriptions of the late eighteenth and nineteenth centuries. This is especially true now that only minor separations (and hence difficult to detect) remain. It has been estimated that probably fewer than a hundred bird species remain unnamed. The usual practice is to name a *type specimen* or *type* *group*, a *type locality*, and perhaps also a type of the other sex. The describer usually lists the various races and specimens with which he has compared his novelty and presents a statement of these comparisons. This may include a statistical treatment and almost always a detailed summary of the ways by which the new form differs from those already named. The range and location where specimens have been found is also given. *Publication* generally means appearance of the new name and description in a "recognized" journal. The *publication date* usually means the actual date of circulation rather than whatever calendar date may be imprinted on the periodical. (Some periodicals, especially European ones, may appear months and occasionally years after the imprinted date.)

Subspecies (often called *races* or *forms*) are rather subjective groups. The various subspecies grade (also called *intergrade*) one into another because they are all one species. The validity of subspecies names therefore becomes rather substantially a matter of opinion because the fineness of the distinctions used varies with taxonomists. While some hold that any constant, recognizable difference is enough to segregate a race, others hold that the difference must be such that a fixed percentage of the race in question can be definitely separated from other races. A common percentage suggested is 75 per cent.

It should be noted that groups additional to subspecies are likewise determined subjectively in varying degrees. The larger groupings (order, family, genus, and their subdivisions) are not found as identities in nature, although they are recognizable in practice. The fact that taxonomists freely push around whole groups, combining some, elevating some, and subordinating others, illustrates the very real difficulties in dealing with manifestations not as yet measurable and definable, and therefore matters concerned largely with subjective determination (e.g., c.f. Mayr and Amadon, 1951; and Wetmore, 1951).

The Number of Species of Birds. In 1758 Linnaeus listed 564 species of birds known to him. Ornithologists recognize about 8,600 today; one count gives 8,590 (Mayr and Amadon, 1951). Nearly 60 per cent of these belong to one order, Passeriformes. How many races there are is a matter of conjecture, but the number "recognized" approaches 30,000. The number will grow or shrink with the fineness of discrimination or opinion. The number of genera of birds also is a matter of conjecture or opinion but probably is between 1,800 and 2,600. In comparison to the bird world, there are about 3,500 known mammals, 5,500 known reptiles and amphibians, and 18,000 known fishes. Animal species of the Phylum Chordata total about 36,000. In contrast to this, the total known species of insects has been suggested as perhaps a million.

Orders and Families of Birds. It was envisioned that with the adoption of the binomial system of nomenclature and use of the 1758 edition of *Systema Naturae* as a beginning, a stability of names and classification would be achieved. This commendable ideal has not been realized and seems unlikely to be reached in the coming years. Part of this instability arises from the constantly increasing knowledge of birds that makes revision in classification necessary and partly from the inherent weakness in any system that depends upon "priority" (and opinion also) for stability.

Two subclasses comprise the Class Aves (Appendix II). Archaeornithes consists of the ancient, reptile-like birds, as exemplified by *Archaeopteryx*. The other subclass, Neornithes, comprises the "true birds." Many of the latter are as extinct as *Archaeopteryx*; in fact, it would be most unusual if more birds had not become extinct in the past 150,000,000 years than the 8,600 living today. Because of the ancientness of their times, but one order and one family of Archaeornithes is known. In contrast, the true birds are divided into 31 orders, of which Passeriformes (the perching birds) is the largest. It has some seventy families. In a way, birds parallel mammals, where among the mammals the order Rodentia far outnumbers others, just as Passeriformes does among the birds. A list of orders and families of birds of the world is given in Appendix II.

SUGGESTED READING

CALMAN, W. T., *The Classification of Animals.* London: Methuen & Co., 1949.

CORY, CHARLES B., and CHARLES E. HELLMAYR, *Catalogue of Birds of the Americas.* Chicago: Field Museum of Natural History, 1918.

COUES, ELLIOTT, *Key to North American Birds.* Boston: Dana Estes & Co., 1927.

DOBZHANSKY, T. G., *Genetics and the Origin of Species.* New York: Columbia University Press, 1941.

GRASSÉ, PIERRE-P., *Traité de Zoologie, Oiseaux*, Vol. 15. Paris: Masson et Cie., 1950.

*LACK, DAVID, *Darwin's Finches.* New York: Cambridge University Press, 1947.

MAYR, ERNST, *Systematics and the Origin of Species.* New York: Columbia University Press, 1942.

MAYR, ERNST, and DEAN AMADON, *A Classification of Recent Birds.* American Museum Novitates, No. 1496, 1951.

MAYR, ERNST, E. GORTON LINSLEY, and ROBERT L. USINGER, *Methods and Principles of Systematic Zoology.* New York: McGraw-Hill Book Co., Inc., 1953.

PETERS, JAMES L., *Check-List of Birds of the World.* Cambridge, Mass.: Harvard University Press, 1931–.

SHARPE, R. BOWDLER, *Catalogue of Birds in the British Museum.* London: British Museum, 1874–1898.

SHARPE, R. BOWDLER, *A Hand-List of the Genera and Species of Birds.* London: British Museum, 1899–1909.

WETMORE, ALEXANDER, *A Revised Classification for the Birds of the World.* Smithsonian Miscellaneous Collections, 117 (1951): No. 4.

3

Bird Adaptations

FACTORS AFFECTING VARIATIONS

For biological purposes, an adaptation may be defined as a variation that helps the animal in surviving and succeeding in its environment (Chapter 9). But caution seems definitely needed in interpreting adjustment to environment: if animals were always in complete adjustment with their environments, it would hardly seem that any could have become extinct. That animals *did* become extinct seems acceptable evidence that adjustments were not always successful. Yet while adaptations are usually considered as related directly to survival, many variations of plumage and some others are associated not with everyday life, for example, but with courtship characters and performances (Chapter 18). It seems obvious enough that our knowledge of birds, great though it may be, leaves much to be learned about variations and their role in the life of the bird. In this connection, it might well be noted that some characters and variations have been termed *nonadaptive* as distinguished from *adaptive* ones. Whether they are or are not can be decided for sure only when bird students have explored all possibilities. As more bird students find out more about birds, belief in the nonadaptive nature of variations tends to disappear. Perhaps it is the incomplete knowledge of the role played by a particular variation that gives the appearance of nonadaptiveness. Every character and every variation clearly seems to offer a subject of research in bird study.

Origin of Adaptations. The hypothesis has been advanced that *structure precedes function*, which holds that among all the variations arising in bird racial history, only those survive that can serve the bird or to which the bird can become adjusted (Murphy, 1936). The principle of *limits of tolerance* (Kendeigh, 1934) seems to be essentially the same.

All species of Tetraonidae (with the single exception of the Attwater Prairie Chicken which is but a subspecies) develop horny "snowshoes" on the feet with the approach of winter (Fig. 3·1). These help increase the bearing surface of the foot in walking over snow. Because the family is boreal in distribution and terrestrial in habit, we can logically assume that the bird walked in the snow before the snowshoe developed. Hence, the feet carried on the function of supporting the body in the snow before the improved structure developed. But perhaps an extension of the toe scales on the foot of an ancestral Grouse made the bearer more efficient than its fellows and in time a complete series of horny plates developed. As a result of this development, the Grouse was able to extend its range and survive in areas where snow abounded during part of the year. In one way of looking at this, therefore, it appears that the structure developed first and that the function fell in line later. But this occurred a long time ago, and we can but conjecture the reasons and processes behind it.

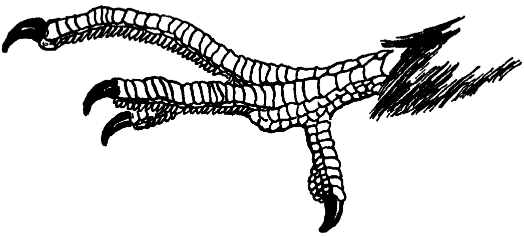


Fig. 3·1. *With the approach of winter, all Grouse (except the Attwater Prairie Chicken) grow a set of "snowshoes" on the toes. In some Grouse living in regions of little snow, the snowshoes may be very small. The foot illustrated is that of a Ruffed Grouse.*

Environmental Adaptation. *Environmental adaptation* means somewhat the same thing as *evolutionary radiation*, a matter to be covered particularly in the chapters on evolution, distribution, and ecological relations. Animals evolving under similar conditions are sometimes called *ecological homologues.* Ordinarily they belong to the same class, but some interclass parallels are evident between birds and mammals, such as Penguins and seals or Moas and ungulates.

The vertebrate competitors of birds (except for other birds) are primarily the mammals, and perhaps they have mutually eliminated one another from many habitats. The true subterranean world belongs to mammals, largely of the order Insectivora (moles) and Rodentia (pocket gopher). The semisubterranean world (sometimes called fossorial) also belongs to the mammals, although a few birds (e.g., Burrowing Owl, Petrel, Bank Swallow, and Kingfisher) have taken a small share of it. The surface stratum under grass and other short plant growth (sometimes called the subvegetation zone), particularly in the open range lands, also belongs largely to rodents. But in the brush and forest, the stratum just above the ground surface belongs largely to the birds, and they even claim much of the forest floor itself. Mammals have not become adapted to flitting or jumping from twig to twig, limb to limb, or tree to tree efficiently enough to challenge the birds. About the best mammals thus adapted for this environment are the tree squirrels among Rodentia and monkeys among Primates. But these creatures move clumsily compared to a nimble bird searching for insects, fruits, berries, and seeds.

The only mammalian competitors of the birds in the aerial world are the bats, and with but a few exceptions, bats use the flying zone only at night when most of the birds are asleep, for few birds have invaded the night period to the extent that they could repress the bats. Birds dominate the marsh and shore more than do mammals. And with their great mobility, once away from land, birds as a class are more successful than mammals in using lakes, ponds, streams, seas, and oceans, although some mammals are well adapted for aquatic life (e.g., whales and dolphins).

It seems entirely probable that, as a general rule, where a major mammal radiation can take place or has already done so, birds have some difficulty in competing with mammals. The Moas evolved on the grasslands of New Zealand (which mammals could not reach) as the avian occupant of the "ungulate niche." Though the Moas, both great and small, occupied the ungulate niche, they were evidently a heavy, ponderous type of animal. The shortening of the tarsometatarsus attests to this—if we may judge by the mammalian world in which it becomes shorter in the "graviportal" type and longer in the fleet, cursorial animals. The tarsometatarsus of the Ostrich measures 49 cm.; the Emu and Cassowary lengths are 39.5 cm. and 32.5 cm., though the birds themselves are only about half the size of the Ostrich. In the Rhea, a fifth the bulk of the Ostrich, the tarsometatarsus is 32 cm. The Giant Moa undoubtedly weighed in excess of 500 pounds, about twice the weight of the Ostrich, and stood 12 to 18 feet high. Yet the tarsometatarsus measured only 45 cm. as compared with the 50 cm. length of the Elephant Bird (*Aepyornis maximus*) that weighed about 1,000 pounds (Amadon, 1947b).

The Penguins of the Antarctic and Subantarctic Zones occupy in the bird world a niche rather substantially similar to that occupied by the seals in the Northern Hemisphere. Both groups have several species of wide distribution in the oceans, and some have even moved into the respective middle and low latitudes. Both occupy a niche characterized by pelagic life during much of the year with return to land during the breeding season. Both have become nearly completely marine, though the Penguins can still walk on land while the seal cannot. The body form of both groups is streamlined. Even the heavily muscled tail of the Penguin parallels that of the seal. The Penguins arose in Antarctica, perhaps in early Cretaceous times. The ancestral forms may have been land birds that became flightless in the remoteness of their insular home from which terrestrial enemies and competitors were barred by distance (Murphy, 1936). The spread of seals into the Southern Hemisphere in recent times (they are found in the Falkland Islands) may foretell an invasion of the Antarctic realm with the result that the mammal will take over from the birds there. But it may be that the Penguin is so well entrenched in its niche that any invasion of *competing* seals has mostly failed. Yet it should be noted that the leopard seal *preys* upon Penguins; a predator, however, is hardly likely to oust its prey, and a predator should hardly be considered a competitor.

STRUCTURAL ADAPTATIONS

Forelimb Adaptations. There seems to be agreement among biologists that the wing of the bird evolved from a walking limb of a terrestrial ancestor. Whether the *immediate* reptilian ancestor had bipedal or quadrupedal locomotion is immaterial at this point. In the course of becoming a wing instead of a leg, the light wrist bones fused into two bones. (Two of the fingers have also disappeared and but three remain.) This fusion of parts strengthens the end of the wing, the part bearing the great primary feathers, and reduces weight at the same time (Fig. 3·2).

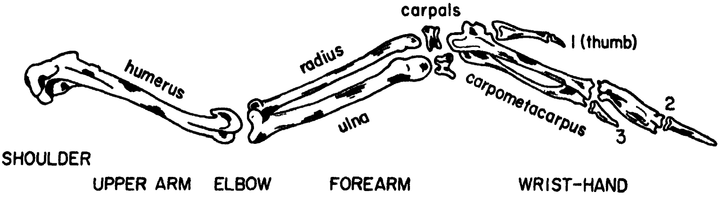


Fig. 3·2. *Bones of the forelimb in birds. The numbers indicate the digits or "fingers."*

In most birds, the skin now covers even the ends of the fingers and thumb, where claws formerly grew, except in the Ostrich (which retains claws on all three fingers) and in some other species or individuals, especially in the young. Three claws may be seen also on the wing of *Archaeopteryx.* Some young birds (e.g., the young of the Green Heron) still use the wing in a quadrupedal manner in climbing about in the vegetation surrounding the nest. The young Hoatzin of South America does likewise; young of common Passerines may do so also. A Parrot, too, may climb about like a four-legged animal, even as an adult.

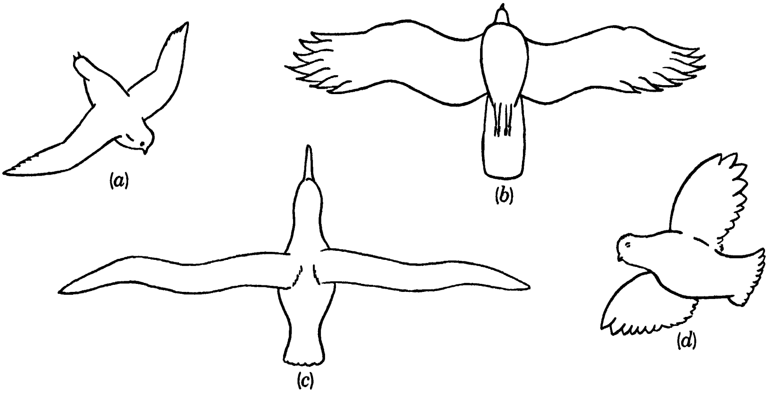


Fig. 3·3. *Four different shapes of wings associated with flight patterns. (a) High-speed, maneuvering wings of a Swift; (b) broad-winged, slotted, over-land type of soaring wings as of a soaring Hawk; (c) long, narrow, over-water type of soaring wings of the Albatross; (d) short, rapid-acceleration type of Bob-white wing.*

The proportionate length of the wing is usually governed by the number of *secondaries* (or vice versa). In some birds, however, a long wing may be the result of longer *primaries,* as in the Chimney Swift. Despite its great wing-spread, for example, an Albatross has only ten primaries, the same number as a tiny Hummingbird. But the Albatross has forty secondaries to the Hummingbird's six. The primaries attach to the finger and wrist bones, the secondaries to the forearm. Additional feathers forming the *alula* belong to the thumb (pollex). As will be seen in the chapter on flight, numerous variations occur in the shape of bird wings, just as numerous flight patterns occur also (Fig. 3·3). Varied but characteristic methods of launching flight or coming to rest also occur.

In addition to the evident flight modifications, on the wings are found a number of ornamentations, of which most occur on the male, a fact that indicates the secondary sexual character of such plumage (Fig. 3·4). Many ducks sport strikingly beautiful wing adornments (Fig. 3·5). The long, spectacular feathers decorating the Birds-of-paradise have a bizarre look. The Waxwing has the wing feathers decorated with waxlike tips.

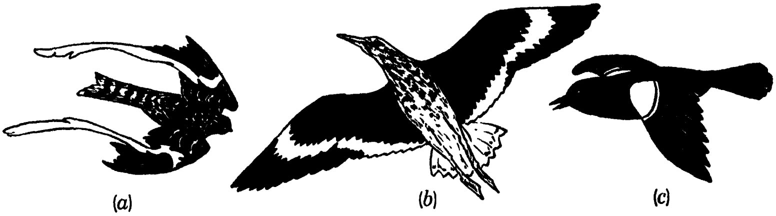


Fig. 3·4. *Wing ornaments seldom take the form of trailing feathers as in (a) the Pennant Nighthawk. More common types are white patches as in (b) the Willet, or colored markings like those (c) of the Red-winged Blackbird. Associated with color patches may be characteristic display habits as in (a) and (b).*

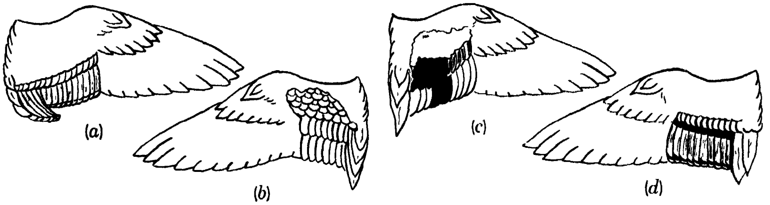


Fig. 3·5. *Many ducks have striking wing pattern adornments. (a) Eider, (b) Golden-eye, (c) Gadwall, and (d) Mallard.*

Tail Adaptations. The chief function of the tail seems to be to oppose the air and thereby to support the rear of the body (Chapter 15). The tail may probably function to some extent as a steering apparatus (as does the rudder in airplanes and ships), but maneuverability is associated largely with flight control through the wings and their muscles, the power plant of birds. Soaring birds have rather broad tails while powerful flyers may have narrower ones (Fig. 3·6). But birds of rapid, direct flight tend to have short tails and somewhat faster wing beats. Swifts, Hummingbirds, and others of fast flight have rather narrow wings and almost no tail. A comparison of the general tail length of Passerine birds indicates an increase in flight speed with decrease in tail length (Table 3·1).

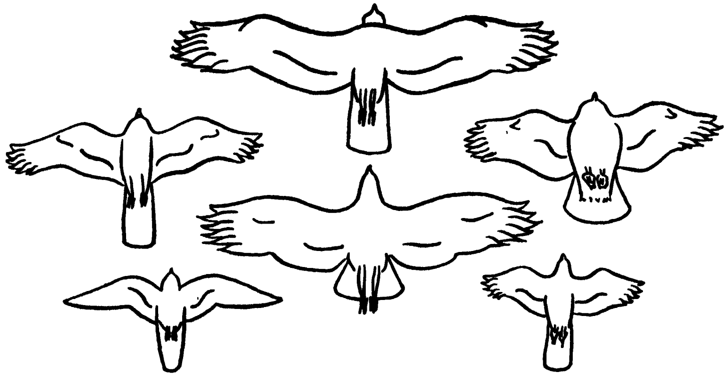


Fig. 3 • 6. *Soaring birds have rather broad tails, often heavily muscled, while fast-flying birds may have narrow tails.*

Table 3 • 1
Flight Speed and Tail Length

Average Flight Speed (from Cooke, 1937)	Length of Tail as a Percentage of Total Length
22	48–52
28	43–47
31	38–42
45	33–37

The fact that many long-legged wading birds fly with the legs outstretched behind is probably of some significance. Most, if not all, are birds with small tails. They are also birds with long necks, so that the projecting of legs behind and neck ahead balance each other (see Fig. 1·15). It is unlikely that the long legs have any great use in steering, although air pressure against them may perhaps help in their support. In any event, birds that hop about quickly from perch to perch hold their legs in a ready position against the body.

The number of tail feathers, with few exceptions, varies from four to twelve pairs (they always appear in pairs in accordance with the bird's *bilateral symmetry*). The Cassowary and Emu have no tail feathers and the domesticated Fan-tailed Pigeon may have twenty pairs. The ancient *Archaeopteryx* had a long tail of twenty vertebrae; some authorities report that each vertebra supported a pair of feathers and some hold that only twelve did so. Increased flight power has been associated with a shortening and fusing of the tail elements until now only a few vertebrae remain separate, the rest being represented by a peculiar bone, the *pygostyle* (called also the plowshare bone).

The feathers are inserted in the fleshy mass of tissue which surrounds the pygostyle. (Fig. 1·7).

Scansorial birds like the Woodpeckers, Creepers, and Woodhewers use the tail as a prop in moving up tree trunks. The Woodpeckers particularly brace themselves with it while drilling holes in trees. The absence of barbs in the tail of the Chimney Swift results in spines which are remarkably effective in helping to support the bird when it clings to a vertical surface.

Just as the wings occasionally bear ornaments, usually in the male only, tails also often bear them. But because the tail plays a less important part in flight, ornamentation is more common and often bizarre (Fig. 3·7). The Motmot has a tail with central feathers peculiarly developed into a trailing, mothlike enlargement. The swallowtails of the Barn Swallow (our only Swallow-tailed Swallow), Arctic Tern, and Swallow-tailed Kite lend grace to their flight.

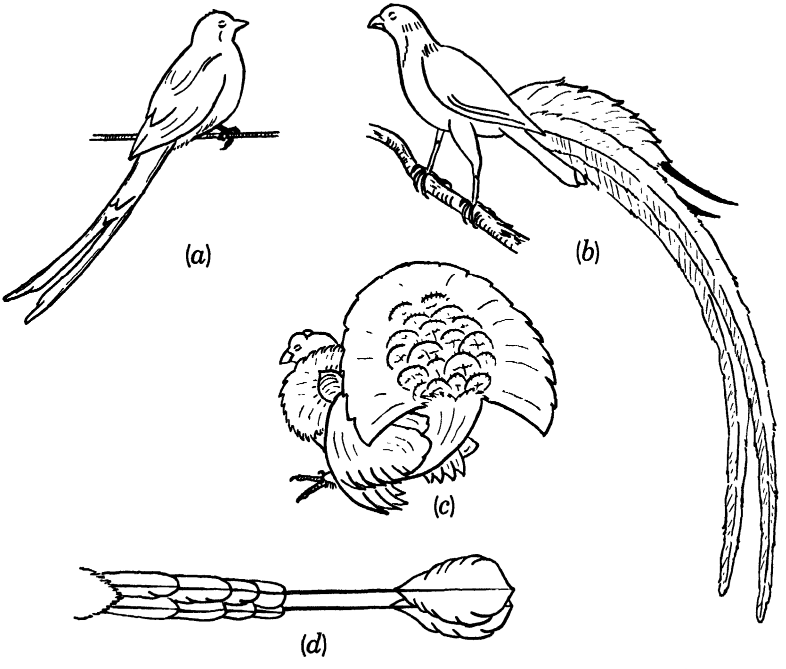


Fig. 3·7. *The tail of the bird often bears bizarre ornamentation. (a) Scissor-tailed Flycatcher of Texas, (b) Paradise Whydah of Africa, (c) Blue Grouse of British Columbia, in full display, and (d) elongated middle tail feathers of the Central American Motmot. (From various sources.)*

The Emu-wren has six long, almost barbless tail feathers which greatly weaken its flight, ornamental though they may be. The breeding plumage of the male Paradise Whydah (Widow Bird), an African member of the Ploceidae, includes tail feathers more than five times the body length, the bird itself being about the size of a House Sparrow. It is said that when these feathers are wet with dew, flight is impossible. The gorgeous tail of the Lyre Bird results from special modifications of the outer pair of feathers, which outline the lyre, and its six pairs of inner ones, which resemble lyre strings. The European Black Cock (*Lyrurus*) has recurved, lyre-shaped outer tail feathers. The Lyre-tailed Honey-guide has similar tail feathers, but the outer ones vibrate in the air stream to produce sound.

The ornamental tail of the Peacock involves the upper tail coverts, though the rectrices themselves may supply some support. Males of the family Tetraonidae spread the tail in display, as do some other gallinaceous birds (Fig. 3·7). Many other birds do so also, including some Passerine birds such as the American Redstart and Myrtle Warbler.

Adaptations of Head Structure. The adaptations in the head structure of birds are generally associated with feeding habits, but many superficial characters are associated with breeding seasons. The eyes are situated rather high on either side of the head, which gives the advantage of a wide vision forward, sideward, and backward, covering about three-quarters of a circle (Fig. 4·21).

The wide variety of bills in the bird world shows well the evolutionary possibilities in a single organ (Fig. 3·8). While it is impossible for us to designate any bill as a general type, several bills do appear to be "general purpose" ones. Among these are the bills of gallinaceous birds, and especially the members of Corvidae and Icteridae. They can be used to pick flesh apart, tear chunks out of fruit, seize an insect, crack a seed, or pick up a small object. The bills of many birds, on the other hand, have become so specialized as to be restricted in their use. Thus, the bill of the Crossbill serves admirably for opening pine cones so that seeds may be extracted but is less effective for most other types of feeding. Woodpeckers can chisel open a tree-borer's home, but they have some difficulty picking up small objects. The bills of Warblers and other insectivorous birds are rather poor instruments for cracking seeds, although they are ideal forceps.

Among the water birds occur many noteworthy bills peculiarly adapted to the food habits of the species. The Pelican bill bears a capacious pouch, larger than the gular sac of any of its relatives. Most Ducks have a bill admirably suited for straining food particles from the water, but Mergansers have saw-toothed bills to hold fish.

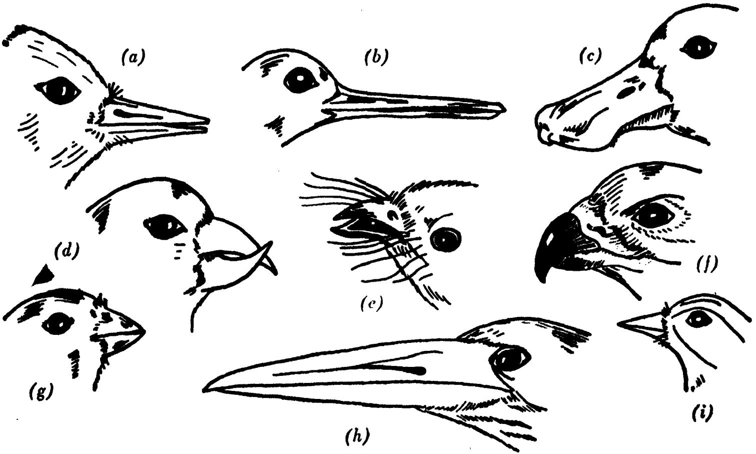


Fig. 3·8. *Some types of bird bills.*

The bill of the Black Skimmer has an elongated and razor-edged lower mandible, longer than the upper one (which resembles the usual type). The bird skims above the water (page 441) with its bill projecting below the surface to scoop up or to pick up organisms (Fig. 3·9). The bills of predatory birds have sharp hooks at the end for tearing flesh of prey into chunks for swallowing. The hooked bill helps also to hold prey, though this is chiefly the job of the talons.

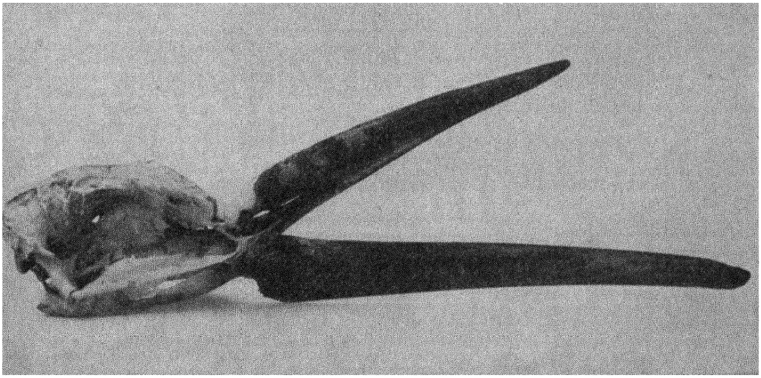


Fig. 3·9. *The bill of the Black Skimmer has a rigid, elongated lower mandible. The short upper mandible opens and closes instead of the lower. (Photograph by Ivan Tompkins.)*

Cormorants and some other predatory water birds likewise have hooked bills.

Some adornments appear on the bill (Fig. 3·10), which is in line with the principle that any especially visible part of the bird may bear ornamentation. The bill of the Puffins is a gorgeous, triangular affair; its color becomes intensified during the breeding season. The Rhinoceros Auklet received its name from a hornlike, breeding-season projection atop the bill (Fig. 3·10). The bill of the Evening Grosbeak changes from yellow to a clear green with the coming of the breeding season.

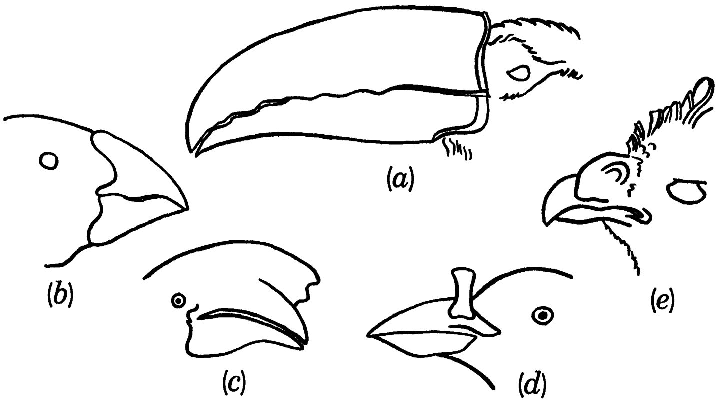


Fig. 3·10. *The variety of bird bills indicates the evolutionary possibilities in this single structure. (a) Toucan, (b) Finch, (c) Hornbill, (d) Rhinoceros Auklet, and (e) Curassow.*

Nearly all birds have skin muscles capable of causing feather erection on the head. It may change the outline, even giving the bird a very grotesque appearance at times. The great variety of crests, plumes, and ornaments is indeed remarkable (Fig. 3·11). Many are found in the male bird only; some are present only in the breeding season. In some species, both sexes possess these adornments, but those of the female are smaller or less spectacular.

The crest on some birds stands erect at all times. Among common birds with permanent crests are the Tufted Titmouse, Cardinal, Steller Jay, and Cedar Waxwing. The Secretary Bird derives its name from permanently displayed plumes at the back of the head that reminded earlier travelers of a bookkeeper and his pens. Sometimes the common name indicates adornment, e.g., "crested," "tufted," or "crowned." Some birds (the Ruby-crowned Kinglet, for example) have a crest that can be flashed at will (Fig. 7·18).

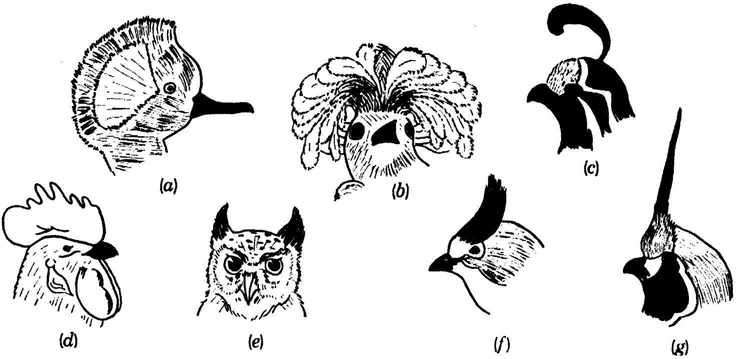


Fig. 3 · 11. *A few examples of the great variety of head plumes, crests, and other adornments. (a) Hooded Merganser, (b) Royal Flycatcher, (c) Valley Quail, (d) Domestic Rooster, (e) Horned Owl, (f) Tufted Titmouse, and (g) Mountain Quail.*

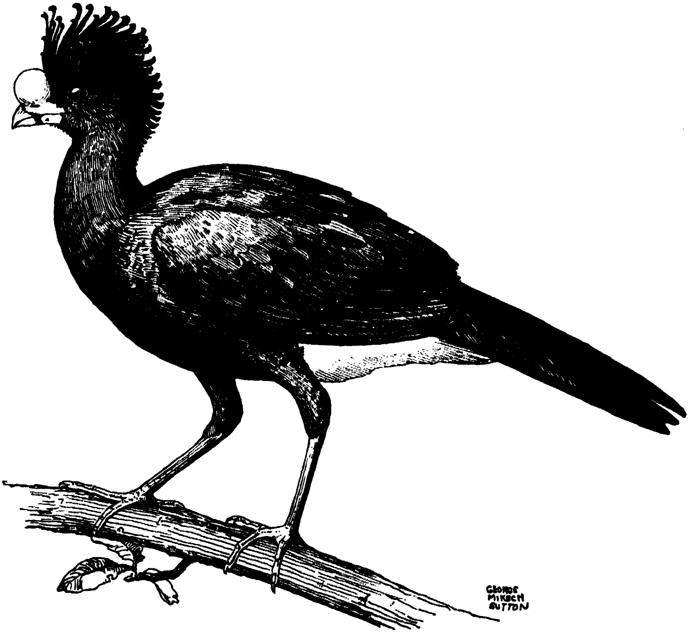


Fig. 3 · 12. *The Crested Curassow, or* Faisáno Real, *of Mexico bears both a crested head and an adorned bill. The entire bill, adornment and all, grows more intensely yellow with the coming of the breeding season. (By permission from* Mexican Birds, *by George Miksch Sutton, p. 166. Copyright, 1951, University of Oklahoma Press, Norman.)*

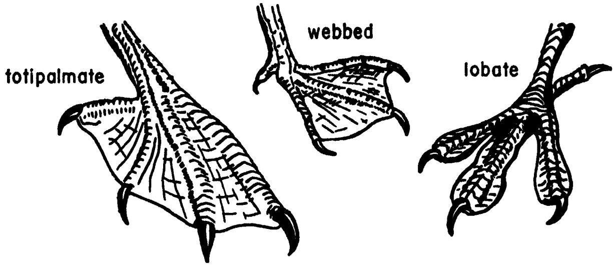


Fig. 3 • 13. *Some types of feet in birds.*

The common barnyard Chicken wears large excrescences on the head in the form of combs and wattles. The male has them much larger than the female. The Turkey has a bare head with warty growths. In at least one bird, the Bell-bird of South America (a member of the Cotingidae), the head adornment has been reported to be inflatable. The colors of the various wattles and similar adornments vary from red and yellow to orange and occasionally even to blue. The "bulbous nose" and bill of the *Faisáno Real* are yellow, though the crest is black (Fig. 3·12).

Scavenger birds like the Vultures and Condors usually have bare heads, perhaps because plumage on the head tends to become excessively "soiled" in the Vulturine way of life.

Foot Adaptations. The shape, structure, and condition of the foot is related to life habits, and the foot varies no less than the bill (Fig. 3·13, Fig. 1·12). Although a five-toed hind foot probably belonged to the reptilian progenitors of birds, no birds (not even fossil ones) have more than four toes. Two is the smallest number of toes found among birds; even as few as three toes are not common.

Scales cover the feet of birds; probably they have been retained since reptilian days. Several different types of scale coverings can be recognized, varying from numerous scales in gallinaceous birds, Shorebirds, and others to a single horny covering in the American Robin and its relatives (Fig. 3·14).

Toes terminate in *claws* that vary with the habits of the bird, just as the foot itself does. The Chicken and other scratching birds have strong, nearly straight claws. Perching birds have slender, sharp-pointed ones. The claws of some water birds may be much reduced, but not so among most land birds. The claw of the rear toe on some walking Passerine birds (the several species of Longspur show this well) is especially elongated, probably to give additional bearing surface upon the ground and to prevent rearward tipping. Toes of perching birds are rather unsuited to ground travel, or if modified for

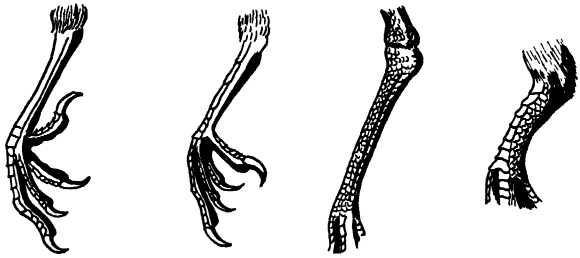


Fig. 3 • 14. *The foot of the bird bears a light protective covering of scales, probably as a still-useful inheritance from reptilian times.*

ground work (as in many Icterine species), their perching facility may be reduced.

Two separate adaptations of the foot for swimming have been evolved, the common one being the webbed (*palmate*) foot, as in the Anseriformes. In this order, webbing involves only three toes, the rear toe remaining free. In Pelicans and their allies, however, the webbing includes all four toes, a condition called *totipalmate.* The second development of a swimming foot is by means of lobes (*lobate*) which grow out from each side of the toes. These lobes fold together as the foot draws forward and flatten out against the water during the backward, power stroke. In the webbed foot, the toes are drawn together in moving forward and spread out for the power stroke.

Predaceous birds have the toes tipped with strong curved claws, the whole forming the characteristic *talons.* These are especially capable as grasping and piercing devices for catching and holding prey.

Wading birds, including Shorebirds, have long toes that give greater control in supporting the towering body and give greater bearing surface on the soft mud bottom. The long toes of the Jacana are especially noteworthy examples of elongation for supporting the body on a soft footing. The Jacana can walk over aquatic vegetation, a feat made possible by the long toes which can spread across a large leaf or several nearby ones. The Gallinules have some faculty also for walking on lily pads and other vegetation, and most Shorebirds show similar, though not so efficient, tendencies.

Most birds carry three toes forward and one backward. The cursorial type of foot found in the Ostrich has two toes, both toes directed forward. One of these toes is small, which shows an evident evolutionary trend toward a single-toed, running foot, a singular parallel to the evolution of the horse. The toes of Chimney Swifts are especially adapted for grasping vertical surfaces. Woodpeckers, too, can hold to vertical surfaces; they have two toes pointing forward and two backward, though some species have only three toes in all, two forward and one backward. A few birds, like the Osprey and Horned Owl, can rotate the outer toe to present two forward and two backward or three forward and one backward. The "yoke-toed" foot of the Cuckoos and their relatives has two toes forward and two backward in a condition termed *zygodactyly.*

The length of the legs in birds varies more or less according to their general life pattern. Marsh, shore, and wading birds have the legs lengthened in order to hold the body above the water. As a compensation, the neck has lengthened so that the bill will still reach the ground. Some exceptions do occur, however, as might be expected. The Woodcock, although a Shorebird, has short legs in token of its terrestrial, woodland habits. The legs lengthen among running birds to increase speed over the ground, and the neck of running birds has become correspondingly elongated. The Road-runner of southwestern North America shows the same relationship of long legs and long neck; its Cuckoo relatives, by contrast, have short legs and necks.

Other adaptations among swimming birds are worthy of remark. The plumage is heavy and "wet proof." Its thickness supplies a high insulation factor, needed more in the highly conductive water medium than in air. No doubt the feather coat also helps to increase buoyancy. Allied to the insulation afforded by the feathers is a heavy layer of fat immediately under the skin, which provides an additional insulation layer, just as it does in sea mammals. The feet of many aquatic groups (as in the Penguins, Loons, and Grebes) have shifted to the stern where they are more efficient paddles than they would be if they were set farther to the front. The Loons and Grebes cannot stand well on land, but Penguins can do so in an erect position. This erect stance gives to them a comical, human aspect.

SUGGESTED READING

*ALLEN, ARTHUR A., *The Book of Bird Life.* New York: D. Van Nostrand Co., Inc., 1930.

*ALLEN, GLOVER M., *Birds and Their Attributes.* Boston: Marshall Jones Co., 1925.

*ARMSTRONG, EDWARD A., *Bird Life.* New York: Oxford University Press, 1950.

EVANS, A. H., *Birds.* London: Macmillan & Co., Ltd., 1899.

*FISHER, JAMES, *Birds as Animals.* London: William Heinemann, Ltd., 1939.

*FISHER, JAMES, *Watching Birds.* Harmandsworth, England: Penguin Books, Ltd., 1951.

*HESS, GERTRUDE, *The Bird: Its Life and Structure.* New York: Greenberg, Publisher, 1951.

*NEWTON, ALFRED, *A Dictionary of Birds.* London: Adams & Charles Black, 1893–1896.

*PETTINGILL, OLIN SEWALL, *A Laboratory and Field Manual of Ornithology.* Minneapolis: Burgess Publishing Co., 1956.

*PYCRAFT, W. P., *A History of Birds.* London: Methuen & Co., 1910.

*THOMSON, J. ARTHUR, *The Biology of Birds.* New York: The Macmillan Co., 1923.

4

Body Structure and Operation

An intimate relationship exists between anatomy, the study of body construction, and physiology, the study of body operation. Hence, it seems profitable in studying the anatomy of the bird as a living organism to relate structure to function. Physiology itself is related rather intimately to ecology, for the former deals with the *internal* relations of the body and the latter with the *external* ones. Though ordinarily clear enough, it is hard (or even impossible) sometimes to recognize the point of transition from physiology to ecology or at times to separate one from the other.

GROSS ANATOMY

Skeletal Structure. The skeletal structure of the bird consists primarily of bone and cartilage, along with the necessary soft tissue (largely connective) to fasten the parts to each other and to the rest of the body. Birds use cartilage much less in the skeleton than do other vertebrates, chiefly because the bird skeleton must be rigid for service in flight. *Hyaline cartilage*, now forming the *tracheal rings*, has become calcified and is sometimes termed *calcified cartilage*, though it is still hyaline. *Fibrous* and *elastic* cartilage is used sparingly for filling in at the ends of bones or for partial support of other structures.

Bone is the most important feature of the skeletal system and reaches a high specialization with respect to economy of material in the bird; it is far more rigid than cartilage. The bone is living tissue in the sense that nerves and blood vessels permeate it. The skeleton

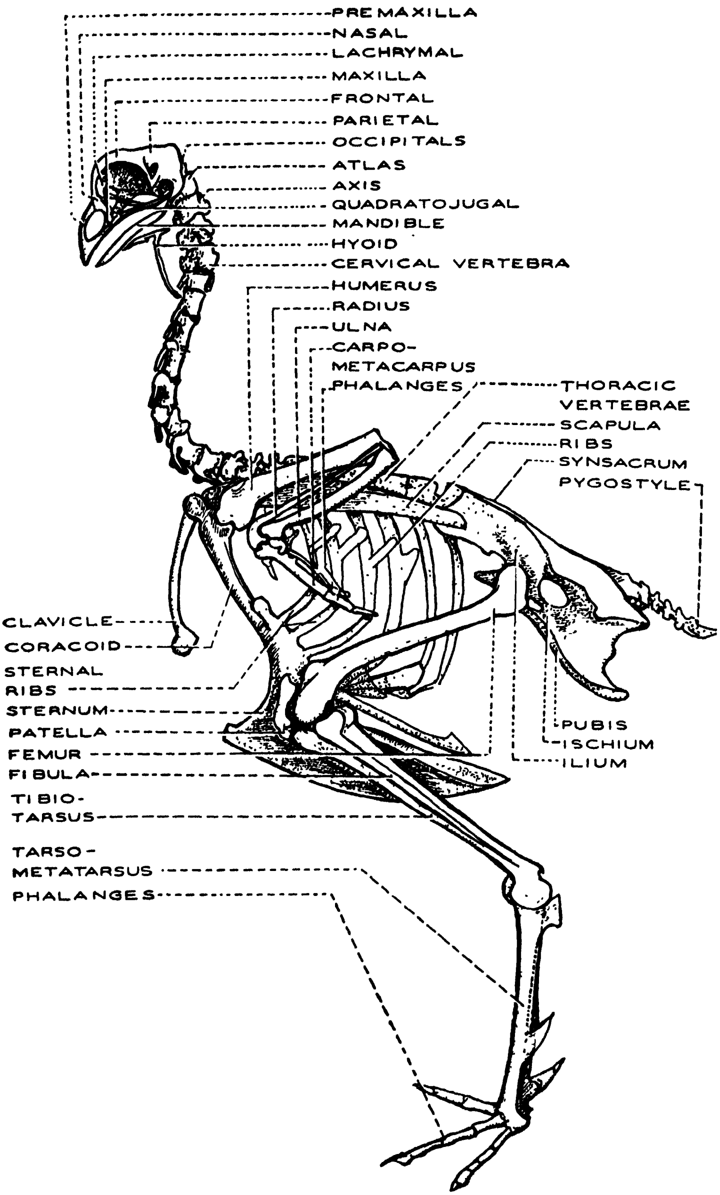


Fig. 4 • 1. *Skeleton of the Domestic Fowl. (By permission from* Textbook of Zoology, *by George Edwin Potter. Copyright, 1938, The C. V. Mosby Co., St. Louis.)*

serves four uses in bird life: (1) providing a supporting framework for body parts, (2) supplying solid attachments for muscles, (3) furnishing leverage for movement, and (4) supplying protection to delicate tissues. Its role in avian red blood-cell production is not clearly known.

The skeleton acts as an internal framework or scaffolding, somewhat as a steel frame reinforces and supports the masonry, brick work, and trim of a skyscraper (Fig. 4·1). The wings, for example, carry most of the weight of the body when in flight, while the legs carry all of it when walking, standing, or perching. Even in water, the skeleton maintains the relatively uniform shape of the body, though support is transmitted through the body itself rather than through the limbs.

The muscles of the body usually attach to the skeleton through flesh or tendons, their fixed end being the *origin*, the movable one the *insertion*. Thus the contraction of the muscle pulls against the rigid skeleton to cause movement at the insertion. Correctly speaking, muscles perform by contraction only; hence, additional muscles or some retractive forces must be present to reverse the contraction. The places of attachment often become flattened, ridged, or otherwise much increased in surface area for greater attachment power of the

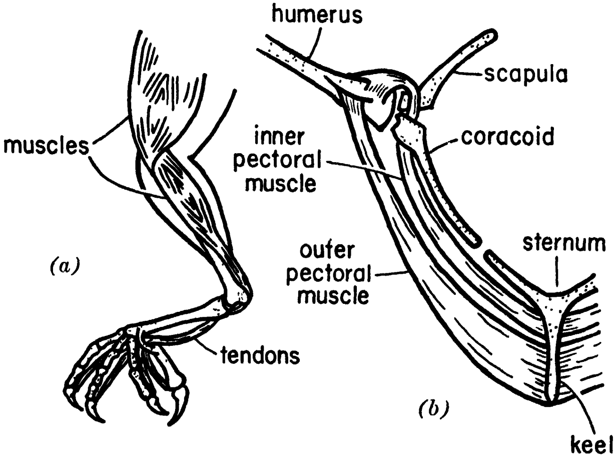


Fig. 4·2. (*a*) *The leg and toes are operated by muscles and tendons. Those operating the toes pass behind the tarsal joint and through the annular ligament to insert on the respective toes. Roosting causes tension on the tendons by bending the "heel and knee" joints so that the toes firmly clasp the perch.* (*b*) *Bracing of the pectoral girdle and the muscles that move the wings.*

muscle. Variations in shape of the bones under the influence of muscle attachment become very great indeed, and each group and even each species tends to have bone variations such as ridges, crests, tuberosities, and processes so characteristic as to make most larger bones and many smaller ones identifiable, sometimes to the species. The most elaborate of these bony modifications for muscle attachment appears in the *thoracic basket* of the bird. The *sternum* has a greatly developed *keel* for the attachment of the enormous flight muscles, so that the muscles operating the respective wings pull against each other.

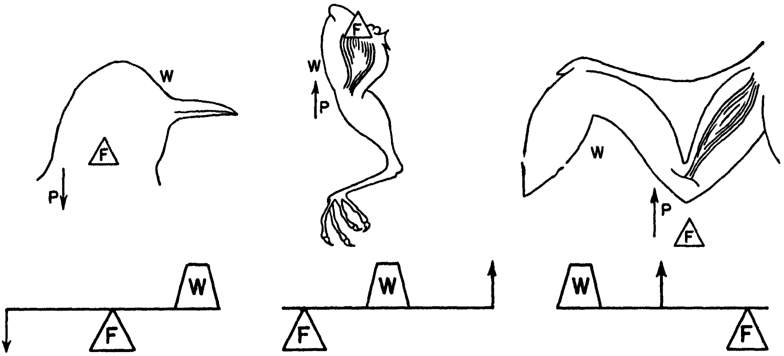


Fig. 4·3. *Muscles perform their work by using levers of the first, second, or third class as indicated in these three examples. The arrow shows the direction of power* (P), W *indicates the weight, and* F *the fulcrum.*

The flat ribs contribute to the streamlining and lightness of the body by reducing the need for padding over the ribs. The sternum is also braced against the wing bones themselves through the rib structure and pectoral girdle (Fig. 4·2). The muscles do their work through systems of "cables, pulleys, and levers" in accord with physical principles (Fig. 4·3).

The *cranium* that protects the brain from injury shows clearly the protective function of the skeleton. In the same way, the *vertebral column* protects the *spinal cord.* The *axial skeleton* consists of the skull, ribs, sternum, and backbone, while the *appendicular skeleton* includes the remaining bony structure.

The skull of the bird shows most strikingly the trend in body structure among birds for reduction in weight by fusing, thinning, and eliminating parts. The many bones comprising the skull can be distinguished fairly well in embryos and young birds. But by the time adulthood is reached, they have fused so completely that it is difficult

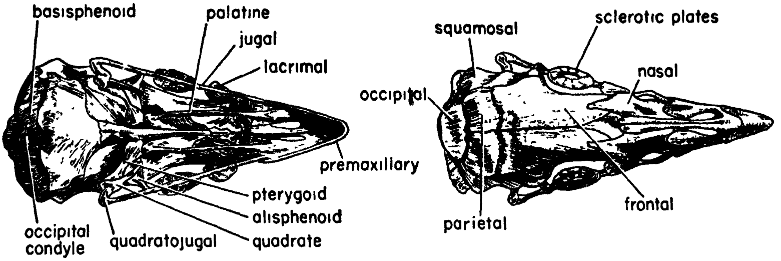
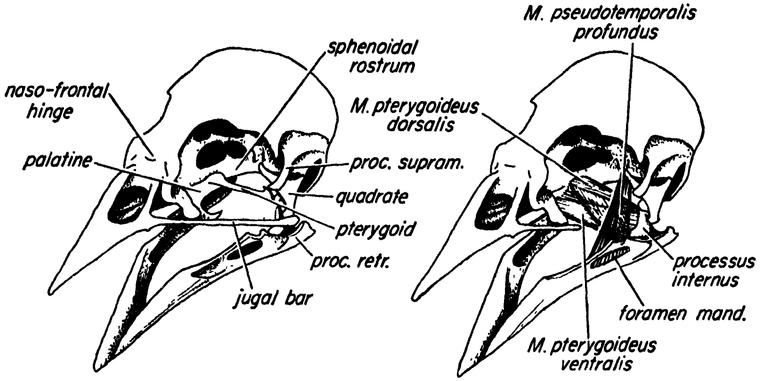
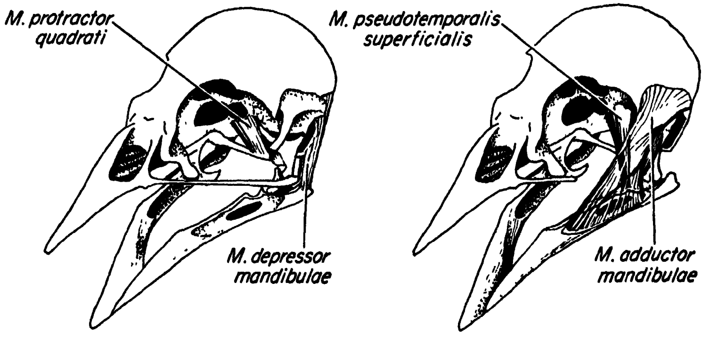


Fig. 4·4. *The various separate bones of the skull (Domestic Chicken) fuse during growth, and most of the sutures and individual bones are not distinguishable.*



THE KINETIC SKULL

PALATINE RETRACTORS



PROTRACTORS (Gaping)

ADDUCTORS (Seizing)

Fig. 4·5. *The function of the bones and muscles shown in this illustration of the "kinetic" skull. (From William J. Beecher, "Adaptation for Food Gathering in the American Blackbirds,"* Auk, *68(1951):414.)*

or impossible to distinguish most of them except by location (Fig. 4·4). Many of the old reptilian (and even earlier) parts have been retained; few have been lost entirely. The lower jaw, for example, still articulates with the skull through the independent *quadrate* bones. The upper mandible usually is rather fixed, but it bends freely at the skull in Parrots. Many young and some old birds, particularly in Paridae, have considerable flexibility between the skull and upper mandible. The lower jaw of the Black Skimmer is held rigid and the upper one opens in feeding (Fig. 3·9). The quadrates themselves articulate with the *pterygoids*, which in turn bear upon the *palatines* and *basisphenoids* (Figs. 4·4, 4·5). An elaborate but efficient muscle system operates the bill (Figs. 4·5, 4·6).

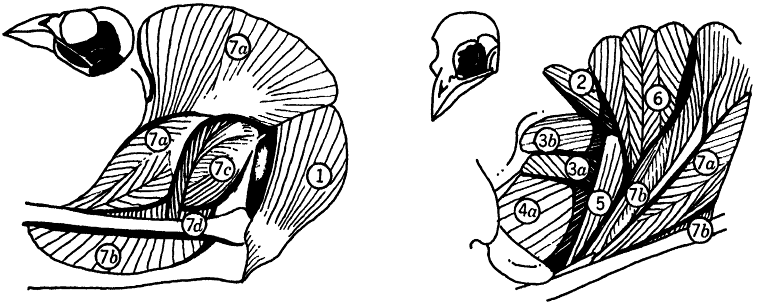


Fig. 4·6. *The muscle pattern of the Cowbird bill.*

Protractors: *Open the bill.* (*1*) M. depressor mandibulae (*depresses lower mandible*); (2) M. protractor quadrati (*elevates upper mandible*).

Palatine retractors: *Draws upper mandible downward.* (*3*) M. pterygoideus dorsalis: (*3a*) anterior, (*3b*) posterior; (*4*) M. pterygoideus ventralis: (*4a*) anterior, (*4b*) posterior (underlies *4a*); (*5*) M. pseudotemporalis profundus.

Mandibular adductors: *Combine to draw lower mandible upward.* (*6*) M. pseudotemporalis superficialis; (7) M. adductor mandibulae: (7*a*) externus superficialis, (7*b*) externus medialis, (7*c*) externus profundus, (7*d*) posterior. (*From William J. Beecher, "Adaptation for Food Gathering in the American Blackbirds,"* Auk, *68*(*1951*)*:418.*)

The brain case of the bird is larger than that of reptiles (because the bird has a larger brain) and has moved backward to make room for the greatly enlarged eyes. Heavy cartilage, evidently commoner in earlier forms, has given way to the stronger bone, and sizable cartilage persists only in the *septum* between the *orbits* and the *ethmoid* region. (Some separate bones largely of cartilaginous origin are the *exoccipitals*, *periotics*, *alisphenoids*, *orbitosphenoids*, and *eth-*

moids.) The skull articulates with the vertebral column through a single *occipital condyle,* which has shifted to the underside of the skull itself.)

The ancestral gill arches gradually have come to serve new functions, though numbers five and six are missing in the bird and number four partially so. The location of the old gill arches in present-day birds follows:

I. Pterygoid, quadrate, and Meckel's cartilage
II. Stapes, hyoid apparatus
III. Hyoid apparatus (Fig. 4·7)
IV. Absent (some may possibly be used in hyoid)
V. Absent
VI. Absent
VII. Tracheal cartilage

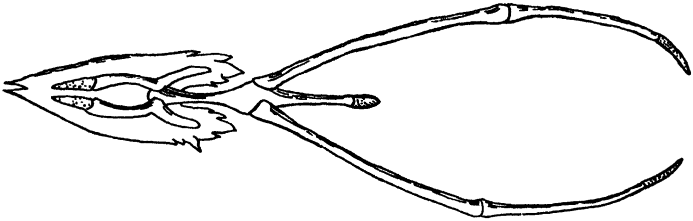


Fig. 4·7. *The third ancestral gill arch has become modified to form the hyoid apparatus supporting the tongue.*

The pectoral girdle of the bird braces the bony basket, especially the *coracoscapular-humeral* joint and *sternum,* against the pull of the great flight muscles. The *coracoids* and *clavicles* serve as powerful braces, while the *scapula* has become narrowed and attached by soft tissue as it lies athwart the ribs. Together the united clavicles are called the *furcula* (also *wish-bone, pulley-bone,* and *merry-thought*).

The *pelvic girdle* consists of the *ilium, ischium,* and the *pubis,* to which are attached by various degrees of fusion the two *sacral* or *pelvic vertebrae* to form a rigid structure for body support in standing and walking.

The forelimb bones of the bird consist of the *humerus* of the upper arm, the *radius* and *ulna* of the forearm, the *carpals* of the wrist, *metacarpals* of the hand, and the *phalanges* of the digits. The humeri, radii, and ulnae remain free, but the carpals and metacarpals show more or less fusion. Only the first (pollex or thumb), second, and third digits remain in the bird. The first supports the alula (which forms a wing slot with the main wing), the second supports the primaries, and the third has largely degenerated or fused with the second (Fig. 4·8).

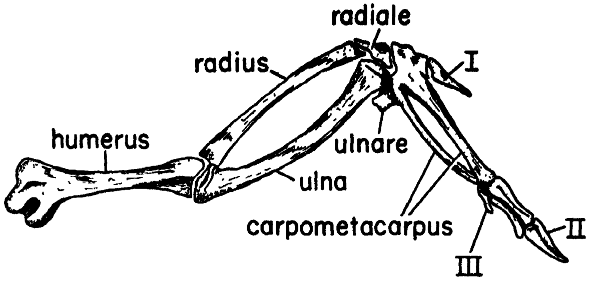


Fig. 4·8. *Wing bones of a bird.*

The *thigh* of the hind limb projects from the pelvic girdle, sometimes almost horizontally. The *knee joint* bends backward as in man (though the knee and thigh usually rest hidden from view in the feathers). The *crus* (drumstick) bends backward at the knee to the *heel joint*, where the leg bends sharply forward to the foot (Fig. 4·9).

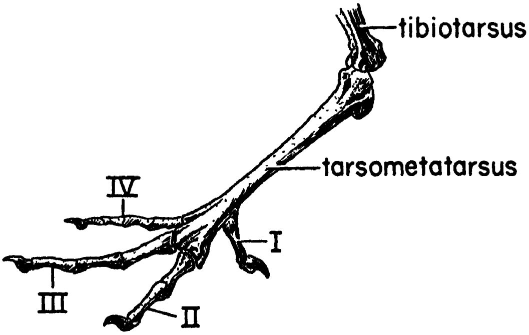


Fig. 4·9. *The leg bones of a bird.*

The lower part of the leg usually has no feathers and popularly is called the *tarsus*, though technically *torsometatarsus* would be better. The bird normally has toes one, two, three, and four; the fifth never appears except as an early embryological transient. The number of *phalanges* characteristically is two for the first toe, three for the second, four for the third, and five for the fourth, one greater than the toe numbering. But various modifications in number occur.

The long bones of the leg are the *femur* (which articulates with the pelvic girdle and at the knee joins the *tibiotarsus*) and the fused and degenerate *fibula*. The lower end of the tibia is fused with several of the upper *tarsal* bones. The remaining tarsal bones are fused to the *metatarsus* to form the *tarsometatarsus*. The *ankle joint* of the bird lies *between* two sets of tarsal bones fused, respectively, to the tibia and metatarsus. This is substantally as in many reptiles but markedly different from the structure in mammals. (Properly we should not call the bones *tibia* and *metatarsus* but should refer to them as *tibiotarsus* and *tarsometatarsus*, respectively, with the *intratarsal* or *mesotarsal* ankle joint lying between them.)

The angles that the joints of the leg make with each other are peculiarly suited for launching the bird into the air by straightening the legs—even as the running mammal can get off to a fast start by straightening the angle of the legs in the initial leap. The tendons which flex the toes run behind the leg. When the bird squats down on a perch, as at roost, the bending of the leg joints tightens the grasp of the toes on the perch. Only when it springs up will the toes open. This also accounts for the forward projection of the raptoral foot to seize a prey or of the perching foot to seize a perch.

Muscular System. Although the muscles of the body (the study of muscles is termed *myology*) serve chiefly to generate motion by contractions that produce power (transmitted through tendons and bones), they serve also for support and protection. The air pressure against the body, tail, and wings supports the air-borne bird, but a layer of muscle underlies the skin; the internal weight rides on the buoying air through the intervening muscles. Air pressure upon the wings and tail gives support transmitted in reverse over the tendons and muscles to the bony framework; it is the muscles that hold the tail and wings firm against air pressure (Fig. 4·10). The muscles, furthermore, offer some measure of protection to internal structures, such as the nerves and bones buried deep in leg muscles.

There exist three kinds of muscle, *smooth* or *involuntary*, *striated* or *voluntary*, and *cardiac*, found, for example, in the viscera, legs, and heart respectively. Muscles like those of the wings or legs are covered by a connective tissue sheath (*fascia*) continuous with the tendons which, in turn, fuse with the *periosteum* of the bone. Several muscle fibers may be ensheathed to form *bundles* of muscles. In the case of the wings, long tendons make it possible for the heavy power muscles to be located at the center of the body (and *below* the wings), which relieves the wings of much immediate, cumbersome weight. Tendons may become *calcified*, as may be seen in the legs of many mature birds—like the drumstick of a Thanksgiving Turkey. As would be expected, the muscle system of the bird shows spectacular adjustments to the needs of flight. The oblique muscles of the abdominal region, well developed in mammals, are reduced. The same may be said for dorsal muscles, reduced in birds in favor of a rigid thorax. The neck, however, has great flexibleness.

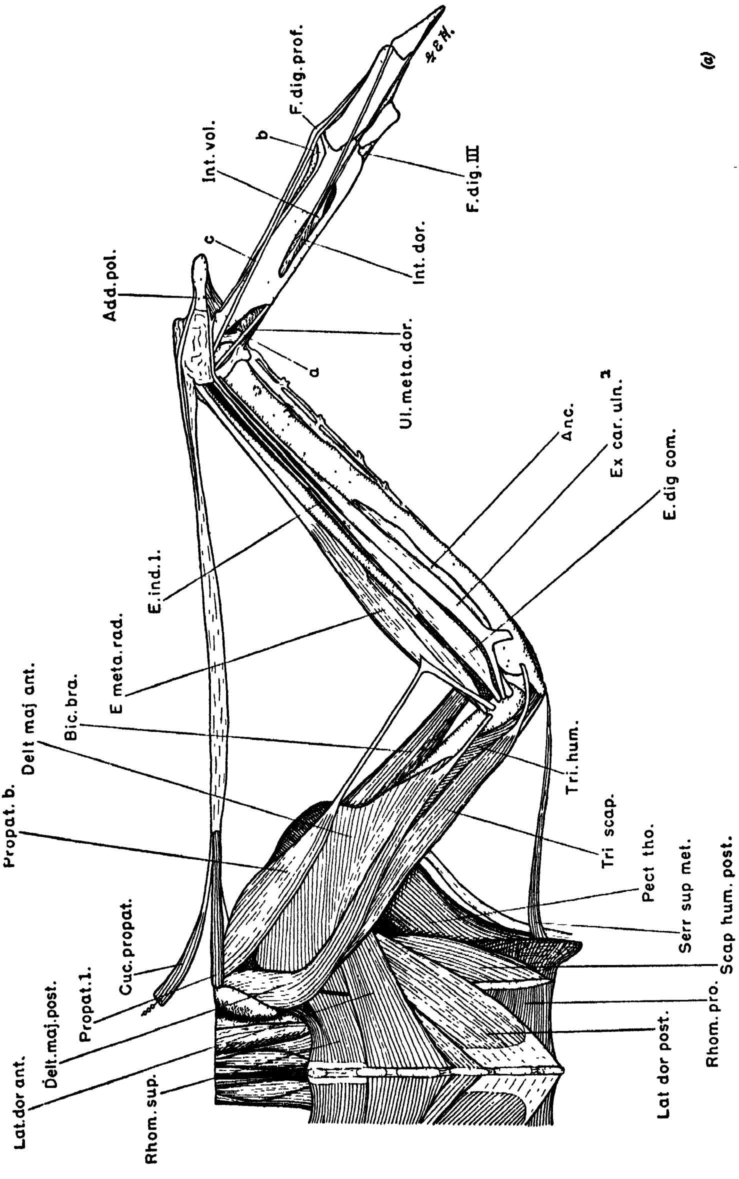

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Fig. 4·10a.

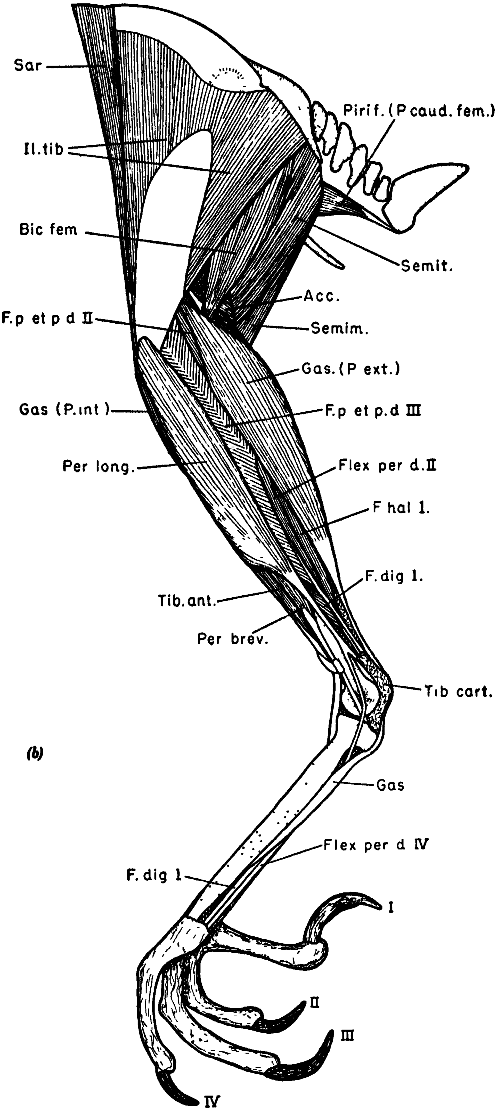

Fig. 4 · 10. *Superficial wing and leg muscles of a Crow. (a) Dorsal view of right wing. (b) View of left leg. (a) From George E. Hudson and Patricia J. Lanzillotti, "Gross Anatomy of the Wing Muscles in the Family Corvidae," American Midland-Naturalist, 53(1953):1–44. (b) From George E. Hudson, "Studies on the Muscles of the Pelvic Appendage in Birds," American Midland-Naturalist, 18(1937):100–108).*

BODILY FUNCTIONS

Digestive Systems. The digestive system of the bird includes the *mouth* with its horny beak, *pharynx*, *esophagus*, *stomach*, *small intestines*, and *cloaca* (Fig. 1·7). The *crop* is part of the *esophagus*, and the *gizzard* is part of the stomach. Food may pass through the digestive system in four hours and sometimes less time. The *tongue* serves chiefly to move the food within the mouth after it has been picked up by the bill and passed into the mouth, usually with the aid of a quick, forward jerk. The *hyoid apparatus*, consisting of the *hyoid* and *branchial* arches (Fig. 4·7), supports the tongue. The tongue is variously modified in many birds according to their food habits (Fig. 4·11). In the Woodpeckers, for example, the prongs of the hyoid apparatus pass back along the under side of the skull and on around to the top, even as far forward as the base of the bill (Fig. 4·12). The tongue itself is barbed and spear-shaped (Fig. 4·11).

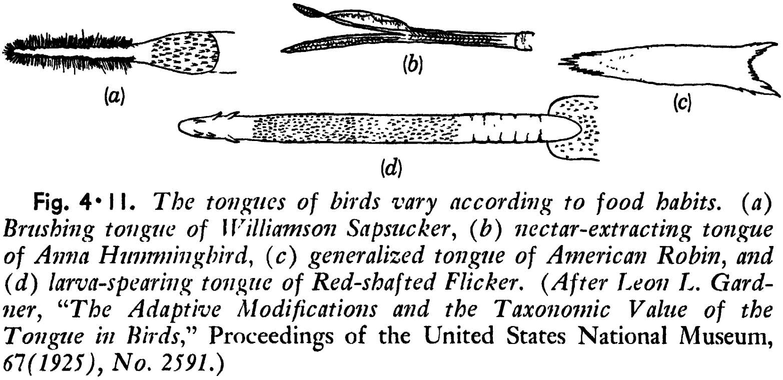

Fig. 4·11. *The tongues of birds vary according to food habits. (a) Brushing tongue of Williamson Sapsucker, (b) nectar-extracting tongue of Anna Hummingbird, (c) generalized tongue of American Robin, and (d) larva-spearing tongue of Red-shafted Flicker. (After Leon L. Gardner, "The Adaptive Modifications and the Taxonomic Value of the Tongue in Birds,"* Proceedings of the United States National Museum, *67(1925), No. 2591.)*

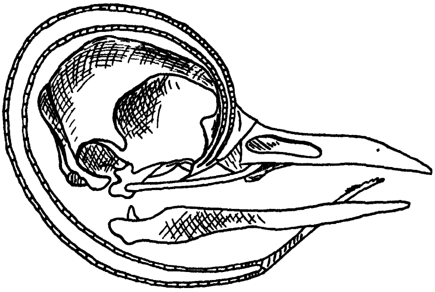

Fig. 4·12. *The tongue of the Woodpecker may be run out beyond the bill because of the long branchial arches. (After Elliott Coues,* Key to North American Birds, *p. 174. Boston: Dana Estes Co., 1903.)*

Table 4·1 lists several functions of various tongues along with examples.

Table 4·1

Examples of Functions of Some Bird Tongues

Function	Example
Probe and spear	Woodpecker, Nuthatch
Sieve	Duck
Suction tube	Sunbird, Hummingbird
Brush	Sapsucker
Rasp	Vulture, Hawk, Owl
Fish holder	Pelican
Finger	Parrot, Finch, Crossbill

Salivary glands are present in some birds, though they are less involved in digestion in birds than in mammals. The Flicker uses its salivary glands to produce a sticky fluid with which to entrap ants on the tongue; other Woodpeckers do so to a lesser extent. The famed "bird's-nest soup" of the Orient is made from the gelatinous product of the salivary glands that Swifts (*Collocalia*) use for holding the nests together. Other Swifts use secretions of the salivary glands in cementing their nests together, as do Swallows also.

From the *pharynx*, the *trachea* leads off to the *lungs* and the *esophagus* to the stomach. The *glottis* in the floor of the pharynx controls the passage of air or food into the proper channel. The esophagus is a collapsible tube equipped with circular muscles which by peristalsis propel the food to the stomach and sometimes regurgitate it. The lower portion of the esophagus in many birds has become enlarged into a storage chamber called the *crop* (sometimes *craw*), which appears chiefly in grain feeders like the Chicken. In some birds, crop glands soften the food (and possibly digest it slightly), but in most birds the crop only stores food before passing it on for digestion. The Hoatzin has a strongly muscular crop for squeezing the juices from succulent leaves. The Pigeon has long been noted for its production of "pigeon milk" by breakdown of epithelial cells in the lining of the esophagus. This milk is chemically rather similar to mammalian milk.

The stomach proper consists of a forward portion merging with the lower esophagus (called the *proventriculus*) into which the digestive glands empty their contents for mixing with the food before it is passed on to the gizzard. The gizzard, the second part of the stomach, is a heavy-walled, muscular organ in seed-eaters and other birds that feed upon hard foods. It contracts powerfully two or three times a minute during digestion. The thick-walled gizzard is aided in grinding the food by gravel or *grit* taken in through the mouth and retained in the gizzard for this purpose. In areas where hard seeds are available, they may substitute for some of the grit; both grit and seeds may become worn down in time by continued use. The size of the grit varies greatly with species, from practically sand in Passerine birds to cobblestones weighing as much as 5½ pounds in the extinct Moas of New Zealand. The grit usually follows rather closely the size of food particles, though averaging larger than the average for food items. Birds pick up grit where it is available; Penguins, for example, gather their gizzard stones from the sea bottom. Some birds, such as Geese, may have especially heavy *grinding discs*, which may be aided by grit. Yet grit does not seem to be an essential item of life, for birds can live without it. But digestion in birds customarily using it seems more efficient with grit than without it.

The muscular condition of the gizzard varies with the food habits of the species. In meat and flesh eaters, the gizzard is soft compared to that of a seed eater; animal foods are easier to break down for absorption. The muscularity varies also with the food habits of the individual. If a bird feeds upon soft foods over a long period, the walls of the stomach will become soft and flabby. An increase in the amount of hard foods will result in increased gizzard strength. The gizzard lining in most birds is shed and renewed continuously like the skin of man. But in the Cuckoo, it is reported to be shed all at once and cast off through the mouth. The male Hornbill wraps food in an envelope secreted by the gizzard lining for presentation to the imprisoned incubating female.

Comparative studies of the crop and gizzard contents indicate that a delay of about an hour ensues between the peak load of the crop and that of the gizzard, which may indicate time taken in softening and mixing foods in the crop and proventriculus, as well as the actual time in passage. (Food may remain in the crop for two to twelve or more hours.) The outlet from the gizzard is at the top, so that gravity tends to hold heavy particles inside. The *pyloric muscles* at the outlet restrict passage of hard and unground foods. Heavy and hard objects, like lead shot, for example, remain in the Duck stomach. Lighter objects and even grit may be allowed through and into the *duodenum*, the forward part of the *small intestine*. Some control apparently can be maintained over the grit, for it may pass out of the gizzard when abundant and be retained by some birds for as much as a year when it is scarce. "Hunger contractions" of the crop, proventriculus, and gizzard may begin before all food is gone, relatively earlier in birds than in mammals. This may be associated with the higher metabolism and "high-speed life" of birds.

The *small intestines* may be rather large and long in vegetation feeders, but they tend to be shortened in most birds. Their chief function is the further breakdown of food and the absorption of nutritive substances; in this they are particularly efficient. The small and large intestines are indistinguishable in birds, but paired *caecums* (useful in cellulose digestion though apparently not essential to life) are attached at the junction of the two. The intestinal tract ends in a *cloaca*, into which the *urogenital system* also empties. Opening off the cloaca in many birds is a structure known as the *bursa of Fabricius*. The intestinal tract (including the cloaca) shortens in accordance with the avian practice of reducing weight where possible. It is shortened most in the more migratory species and in those feeding upon the more concentrated types of foods. Some representative lengths of intestines in inches, as compiled from various sources, are given in Table 4·2.

Table 4·2

Comparative Length of Bird and Intestines

Species	Length of Bird (in.)	Length of Intestines (in.)	Species	Length of Bird (in.)	Length of Intestines (in.)
Barn Swallow	7	7	Prairie Chicken	18	54
House Sparrow	6	9	Kiwi	22	55
Road-runner	22	13	Gannet	36	59
Burrowing Owl	9	15	Anhinga	34	60
Long-eared Owl	15	20	Herring Gull	24	60
Gambel Quail	11	21	Jungle Fowl	27	66
Bob-white	11	22	White-fronted Goose	29	73
Rock Dove	13	32	Sandhill Crane	44	76
Horned Owl	24	38	Shoveller	19	80
Black-bellied Tree Duck	21	44	Whooping Crane	50	80
Black Vulture	25	49	Canada Goose	30	90
Raven	25	50	Trumpeter Swan	65	109
Wood Duck	18	53	Ostrich	90	55 feet

Accessory structures lying against the intestinal tract are the *pancreas*, *gall bladder*, and *liver*. The liver varies in size from about 1.25 per cent to 2.0 per cent of the body weight in various birds (Table 4·3). In the small intestines, *bile* from the liver alkalizes the food mass and also supplies *bile salts* used in fat digestion. The pancreas supplies *enzymes* which convert starches to sugars and others which act further in protein digestion. Other enzymes are added by the glands of Lieberkühn. The chief digestive enzymes and their activities are tabulated in Table 4·4.

Table 4·3
Weight of Various Parts of the Bird Body
(All weights in grams)

Species		Sex	Body	Brain	Thyroid	Adrenal	Heart	Liver	Eyes	Kidneys	Lungs	Spleen	Stomach and Intestines
Ostrich	wt.	M	123,000	42.11	17.33	23.01	1205.00	2050.00	95.26	920.00	2900.00	–	23,133
	%			0.03	0.01	0.02	0.98	1.67	0.08	0.75	2.36		18.81
Loon	wt.	M	1,568	6.38	0.21	0.22	22.24	74.02	4.89	27.61	22.31	–	106.27
	%			0.41	0.01	0.01	1.42	4.72	0.31	1.76	1.42		6.78
White Pelican	wt.	F	3,290	17.95	0.18	0.99	22.12	73.15	12.73	–	29.83	–	255
	%			0.55	0.005	0.03	0.67	2.22	0.39		0.91		7.75
White Egret	wt.	F	1,030	6.12	0.13	0.21	9.25	33.12	–	8.16	33.10	–	135
	%			0.59	0.01	0.02	0.90	3.22		0.79	3.21		13.11
Pintail	wt.	F	670	4.95	0.056	0.08	8.34	30.33	1.70	8.14	17.13	0.89	99.43
	%			0.74	0.008	0.01	1.24	4.53	0.25	1.21	2.56	0.13	14.84
Turkey Vulture	wt.	M	495	9.32	0.115	0.156	10.24	20.99	7.95	10.11	14.73	–	170
	%			1.88	0.02	0.03	2.07	4.24	1.61	2.04	2.98		34.34
Sparrow Falcon	wt.	M	112	2.51	0.016	0.03	1.12	2.52	3.30	1.11	1.52	–	7.43
	%			2.24	0.01	0.03	1.00	2.25	2.95	0.99	1.38		6.63
Ptarmigan	wt.	M	542	2.38	0.026	0.027	7.86	12.99	2.32	3.87	9.61	–	–
	%			0.44	0.005	0.005	1.45	2.40	0.43	0.71	1.77		
Ring-billed Gull	wt.	F	720	8.73	0.05	0.12	7.35	23.51	8.74	7.45	9.13	–	154
	%			1.21	0.007	0.02	1.02	3.27	1.21	1.03	1.27		21.39
Starling	wt.	M	57	1.87	0.006	0.015	0.93	1.99	0.84	0.983	1.07	0.066	5.25
	%			3.28	0.01	0.03	1.63	3.49	1.47	1.72	1.88	0.12	9.21
Starling	wt.	F	58	1.82	0.006	0.011	0.87	2.20	1.06	1.08	1.09	0.041	5.66
	%			3.14	0.01	0.02	1.50	3.79	1.83	1.86	1.88	0.07	9.76
House Sparrow	wt.	M	24	1.03	0.004	0.006	0.41	1.21	0.46	0.345	0.367	0.043	2.70
	%			4.29	0.02	0.02	1.71	5.04	1.92	1.44	1.53	0.18	11.25
House Sparrow	wt.	F	23	1.02	0.004	0.007	0.39	1.09	0.52	0.357	0.40	0.043	2.68
	%			4.43	0.02	0.03	1.70	4.74	2.26	1.55	1.74	0.19	11.65
Bronzed Grackle	wt.	M	82	2.92	0.012	0.013	1.16	2.63	1.92	1.30	1.74	0.051	6.38
	%			3.56	0.01	0.02	1.41	3.21	2.34	1.59	2.12	0.06	7.78

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Table 4·4
Chief Digestive Enzymes and Activity

Chief Enzymes	Source	Activity
Pepsin	Gastric fluids	Protein to proteoses and peptones
(Acids)	Brunner's gland	Acidifies
(Alkalines)	Liver	Alkalizes
(Bile salts)	Liver	Fat digestion
Amylopsin	Pancreas	Starch to maltose
Trypsin	Pancreas	Protein break down to peptids
Steapsin	Pancreas	Fat to glycerol, fatty acids
Enterokinase	Lieberkühn's gland	Activates trypsin
Maltase, Lactase, Invertase	Lieberkühn's gland	Starch breakdown
Erepsin	Lieberkühn's gland	Protein breakdown (peptids to amino acids)

Respiratory System. The respiratory system of birds bears the expected resemblances to that of other vertebrates, but in many respects it is surely the most remarkable of all, for there are many modifications in structure to meet the peculiar needs of a flying organism. It probably has the physiologically most efficient of lungs. The size of the lung varies from 0.20 per cent of the body weight in weak flyers to six or more times that percentage in stronger flyers. Air passes in through the *nostrils* or the open mouth and enters the *trachea* through the *glottis,* a control valve. The united *eustachian tubes,* which equalize air pressures in the ear, open into the *pharynx.* Air passes down the trachea or windpipe, a tube supported by cartilaginous rings. The trachea divides at the lower end into two bronchi, each going to a lung. At or near the junction of the bronchis is the syrinx.

Attached to the respiratory system is a series of *air sacs* that penetrate the various parts of the body. The *interclavicular* air sac in the Domestic Chicken lies in the angle of the *furculum* (wishbone) and against the crop. Lying above this are the *cervical* air sacs. The *pectoral* or *prethoracic* air sac will be found between the two halves of the *pectoral muscles* of the breast. This air sac extends into the hollow humeral bone of the wing and connects also to the interclavicular air sac. Another large air sac penetrates the *oblique septum* and a smaller one forward of it envelopes the *heart.* Lying along the viscera will be found the large *visceral* or *abdominal* air sacs. Though probably best known for the Domestic Chicken, the exact operation of the air sac system is not clear. It functions to carry heat out of the interior of the body and from within the large muscles; it also indirectly helps oxygenate the blood by reinforcing the lung system. All interchange of oxygen and carbon dioxide, however, takes place in the lungs proper, little or none in the air sacs.

Two *primary bronchi* lead from the trachea to the respective lungs where they widen out as the *vestibulum* (with four *ventro-bronchi* arising from each) and the *mesobronchi* (from which arise seven *dorsobronchi*). The *abdominal air sac* arises from the terminal end of the *mesobronchus*; the *post-thoracic* air sac is attached to the *lateral bronchi*, which themselves arise from the lateral surface of the mesobronchus. The abdominal and post-thoracic air sacs are termed

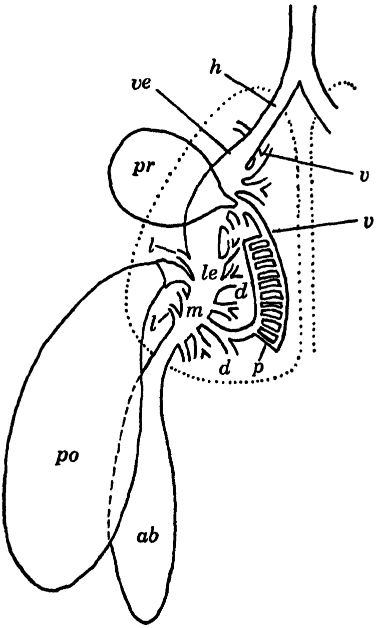

Fig. 4 • 13. *Diagram of the right lung of a bird, ventral aspect. The outline of the lung is indicated by a dotted line. Of the anterior air sacs, only the prethoracic sac is shown. Of the laterobronchi, the only one completely shown is the one which forms the post-thoracic sac; only the beginning of the laterobronchi is indicated. The recurrent bronchi are not reproduced. Only the parabronchi arising from one ventrobronchus branch and one dorsobronchus branch are shown as a series of connected, parallel tubes. Actually, the parabronchi arising from a ventrobronchus anastomose with the parabronchi not only of one but of many dorsobronchi and vice versa.* (h) *primary bronchus,* (ve) *vestibulum,* (m) *mesobronchus,* (v) *ventrobronchi,* (p) *parabronchi,* (d) *dorsobronchi,* (l) *laterobronchi,* (pr) *prethoracic sac,* (po) *post-thoracic sac,* (ab) *abdominal sac,* (le) *"guiding dam."* (*After E. H. Hazelhoff, "Structure and Function of the Lung of Birds,"* Poultry Science, *30(1951):3–10.*)

posterior air sacs. Anterior air sacs (*prethoracic*, *interclavicular*, and *cervical*) arise from the *ventrobronchi* (Fig. 4·13). *Parabronchi*, arising from the ventrobronchi and dorsobronchi, merge (anastomose) so that air may pass through the dorsobronchi, parabronchi, and ventrobronchi (*d-p-v system*) as well as from the mesobronchus in the vestibulum (Hazelhoff, 1951).

Much of the knowledge about bird respiration is conjectural and subject to differences of opinion among anatomists. But in the Domestic Chicken, it is believed that most and perhaps all of the air circulates through the d-p-v system *in the same direction* of passage during both inspiration and expiration. This seeming anomaly is believed to result from constrictions acting as diversion structures at the junction of the mesobronchi and dorsobronchi during expiration and at the junction of the primary bronchi and ventrobronchi during inspiration (Fig. 4·14). Aerodynamic conditions alone control the circulation of air; no valves or sphincters are present. The air in the posterior air sacs passes through the vestibulum-mesobronchus system and some additionally through the d-p-v system. The CO_2 content of the posterior air sacs in the Domestic Chicken averages 2.6 per cent, that of the anterior sacs 5.4 per cent. The latter receive all of their air rather than only a part from the d-p-v system; this accounts for the difference in carbon dioxide content (Hazelhoff, 1951).

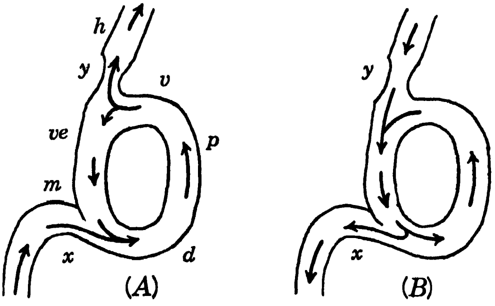

Fig. 4·14. *Greatly simplified model of a bird's lung.* (*A*) *expiration;* (*B*) *inspiration. In both phases the air makes the complete circuit* (ve-m-d-p-v). *Whether the weak current from* ve *to* m *actually occurs in a bird's lung is uncertain.* (*After E. H. Hazelhoff, "Structure and Function of the Lung of Birds,"* Poultry Science, *30(1951):3–10.*)

The strong *thoracic basket* of the bird formed by ribs, sternum, and backbone has sufficient elasticity to expand and contract by numerous respiratory muscles so as to cause *inhalation* and *exhalation* of air. These muscles are controlled by the section of the spinal cord immediately below the medulla oblongata. The hydrogen ion concentration in the respiratory center at the top of the spinal cord and the rise of carbon dioxide pressure in the blood seem to stimulate the breathing rate.

Circulatory System. The circulatory system in the bird consists primarily of the *lymph apparatus*, and the *heart*, *arteries*, *veins*, and *blood* (Fig. 4·15). The circulatory system follows the higher reptilian pattern, but the postcaval vein connects directly to the renal portal system. The heart is large, especially in the more powerful flyers. It may vary from 0.40 to more than 1.50 per cent of the body weight (Table 4·3).

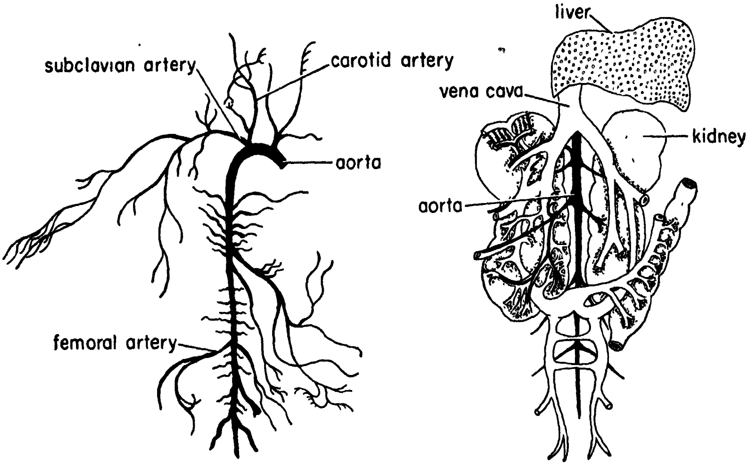

Fig. 4·15. *The bird circulatory system. (Left) Arterio-venous circulation to the liver and kidney; (right) the right aorta only remains and from it rise lesser arteries.*

Blood enters the *right auricle* from the *systemic venous system* and passes into the *right ventricle*, from which it proceeds into the *pulmonary arteries* and then to the lungs. Following oxygenation, the blood passes back to the lungs through the pulmonary veins to the *left auricle*, from which it proceeds to the *left ventricle* and out through the *right aorta*. There is no complete aortic arch in birds; the right half of the fourth arch persists and the left customarily disappears (Fig. 1·11).

The blood which passes out through the *arterial system* goes through it to all parts of the body. The arteries diminish to *arterioles* and finally *arterial capillaries,* which merge with the *venous capillaries.* These increase in size to become *venules* and finally *veins* for returning blood to the heart. The part of the venous system operative in the viscera, particularly in returning the blood through the great liver, is the *hepatic portal system.* That gathering blood from the lower limbs is the *renal portal system,* and the whole is called the *systemic venous system.*

The Blood. Blood arises from the mesoderm and consists of the plasma, a slightly alkaline (pH 7.5) fluid, and the corpuscles carried in it. It is reported to form about 6.5 to 8 per cent of the body weight. Two kinds of corpuscles are found in birds, *red* (*erythrocytes*) and *white* (*leucocytes*). Blood contains salts and other compounds, so that it is a complex substance of slightly higher specific gravity than water.

The enucleated red cells carry oxygen by means of *hemoglobin* (plasma may dissolve some oxygen also). From 2,000,000 to 7,645,000 erythrocytes per cubic millimeter have been reported for birds; large birds have fewer per cubic millimeter than small birds. The average erythrocyte measures about 12 microns long by 6 microns wide, which is substantially larger than in man. The red cells of the Osprey are the largest reported in North American birds (16 microns) and those of the Carolina Chickadee (6.0 microns) the smallest (Bartsch *et al.,* 1937). The leucocytes are larger than the erythrocytes and are present in smaller and more variable numbers. They serve chiefly to combat disease organisms (in the course of which they increase greatly in numbers) and to assist general body repair operations. In addition to the corpuscles, certain other bodies in the blood known as *thrombocytes* act during a case of injury to form a blood clot over a wound. The blood of a bird usually clots within 4 to 5 minutes.

The plasma is a very complex fluid consisting of 80 per cent water and containing at various times dissolved *food particles, waste products, hormones, enzymes, antibodies, fibrinogen,* and other compounds needed in the body. All these things carried in the blood stream are taken up from and given off to the body tissues by *osmosis.* Hence, all substances for transmission to the tissues must be in solution.

The fluid of the open lymph system is *lymph,* closely allied to blood plasma, which contains white corpuscles. There are lymph nodes variously placed throughout the body of most birds (absent in Galliformes and Columbiformes, but some are found in most water birds). Lymphoid structures in the bone marrow of some birds may compensate for lack of nodules. Lymph collects in *lymph vessels* for return to the blood-vascular system.

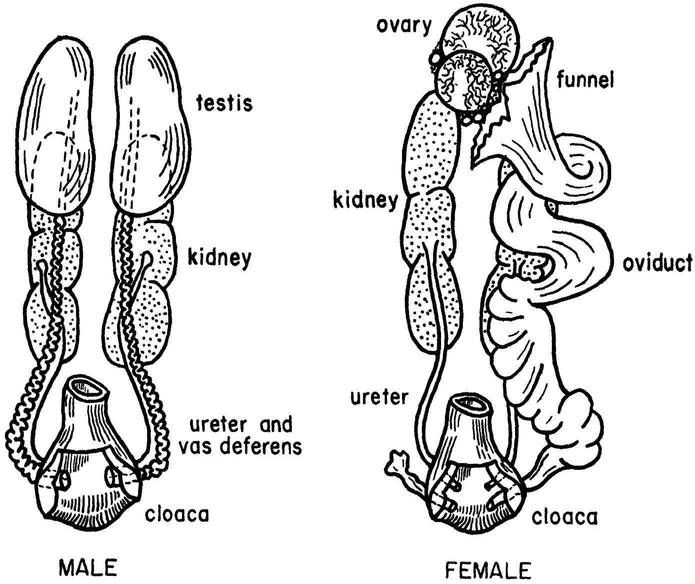

Fig. 4·16. *The urogenital system of the bird (Domestic Chicken) in ventral view.*

Excretory System. Although the unused parts of food in the digestive tract are eliminated directly through the cloaca, the term *excretory system* customarily applies to the *urinary apparatus* (Fig. 4·16). It is involved intimately with the genital system and directly in the excretion of the wastes of *metabolism.* We must not forget, however, that a large measure of metabolic waste is eliminated through the respiratory system as carbon dioxide and perhaps other gases. Furthermore, waste products are deposited in the developing feather and pass to the outer world at the next molt.

The avian kidney (*metanephros*) is packed into the caselike under side of the pelvis. Three parts can be identified, the *anterior*, *middle*, and *posterior lobes.* The blood carrying metabolic wastes passes from the renal artery and renal portal system into the kidney and into a capillary loop, the *glomerulus*, surrounded by a cup called *Bowman's capsule.* The whole is called the *renal corpuscle.* The metabolic wastes pass from the blood through the thin walls of Bowman's capsule into a *collecting tubule.* The urinary wastes in the bird contain little liquid and pass on into the cloaca as semisolids, which are chiefly *uric acid* rather than *urea.* The urinary wastes dry and harden on contact with air and may be recognized as a whitish deposit on the fecal droppings. A bladder is not found in birds.

Reproductive System. The reproductive system is considered further in Chapter 6, so that only its anatomy need be given here (Fig. 4·16). The two *testes* of the male lie forward of the kidney and immediately under the back. The *sperm* is produced in the testes and passes to the cloaca through the *deferent ducts.* There is no copulatory organ in most birds; a *genital papilla* serves as the end of the deferent ducts. In Ducks and some other birds (Ostrich, Cassowary, Emu, Kiwi) a penis is present, but other birds copulate by direct contact of the cloaca of the male with that of the female. The sperm is long and cylindrical and terminates in a motile tail by which it propels itself (Fig. 6·1).

In the nonbreeding season, the ovary looks like a small mass of grapes, the mass being formed of undeveloped *ova* or *eggs.* Seasonally they develop by addition of yolk while within the ovary, from which they break out at daily or longer intervals to pass down the oviduct to the cloaca, from which the final egg is laid.

Endocrine System. The animal body regulates its actions through the nervous and *endocrine systems* (Fig. 4·17). There are several endocrine *glands* within the body that secrete *hormones* into the blood stream to act as regulators of bodily functions through excitation or inhibition. These glands are *thyroid*, *parathyroid*, *pituitary*, *gonads*, *adrenals*, *isles of Langerhans*, and possibly the *thymus.* Adrenal and thyroid glands have shown no significant sex difference (Hartman, 1946).

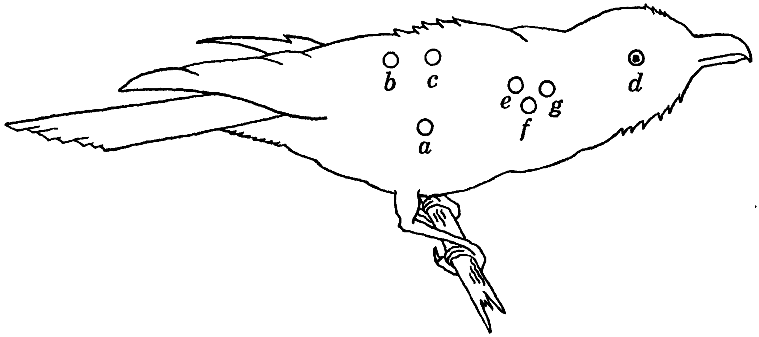

Fig. 4·17. *The endocrine system of the bird in its approximate position. (a) Isles of Langerhans, (b) gonads, (c) adrenals, (d) pituitary, (e) thymus, (f) parathyroid, (g) thyroid.*

The thyroid gland regulates metabolism; its secretions are also necessary for proper growth and sexual development. The parathyroids are two small bodies fastened to the lower part of the thyroids and concerned with calcium metabolism and perhaps with other functions. The pituitary (*hypophysis*) produces several secretions; those of the *anterior pituitary* regulate the other glands of the body and probably also have some body-regulation functions of their own. The hormones produced by the *posterior pituitary* may have some metabolic regulatory function. The pituitary gland also regulates growth. The gonads serve as endocrine glands through hormones secreted by the *interstitial cells* in addition to their primary reproductive function.

The adrenal (suprarenal) gland secretion, *adrenalin*, controls the glycogen supply of the blood, the heart rate, and perhaps the constriction of blood vessels. The intimate connection between the adrenal gland and the nervous system permits nervous tension, as occurs in emergencies, to be transmitted quickly to the adrenals for immediate stimulation. The isles of Langerhans are cell masses within the pancreas that produce a hormone, *insulin*, which regulates carbohydrate metabolism. The thymus gland appears in the neck region of the embryo but becomes much reduced by hatching time. Its function is not known; it may actually be a lymph mass rather than a true endocrine gland.

Table 4·3 gives some samples of the weights of various body organs and parts of the bird.

THE NERVOUS SYSTEM AND THE SENSE ORGANS

Nervous System. The body of the bird has a well-developed nervous system. Birds respond to stimuli more rapidly, generally speaking, than do most other vertebrates. For all practical purposes, birds carry on much of their life by instinct, because their reasoning ability is low. Some writers have called birds "feathered automatons," but this statement pays little tribute to their intellectual capacity. Experiments to test their intellectual capacity have shown that among others, the Corvidae rank high, so that the expression "smart as an old Crow" does have some merit. The size of the brain varies with that of the bird and presumably with its general level of intelligence. That of the Crow weighs 9.3 grams, more than that of the larger Sandhill Crane (8.58 grams). Other brain weights range from about 0.564 grams in the Canary (15 grams body weight) to 42.11 grams in the Ostrich (123,000 grams body weight) (Quiring, 1951).

The nervous system as a whole consists of sensory organs and the *central* and *sympathetic* (*involuntary*) nervous systems. The central nervous system has two parts, the *brain* and the *spinal cord*. The brain in reality is an enlargement of the forward end of the spinal cord. The great sense organs of sight and hearing and the seat of many other mental faculties are located in the brain.

The brain itself consists of several parts (Fig. 4·18), the rearward one of which is the *myelencephalon* (*medulla oblongata*). It grades imperceptibly into the spinal cord. The next forward portion is the *metencephalon*, formed chiefly of the *cerebellum*, which is comparatively large in birds. The *mesencephalon* lies ahead of the metencephalon and controls vision through the *optic lobe*; it also concerns itself with hearing. Still farther forward lies the *diencephalon*, which serves chiefly as a relay center. The front part of the brain, *telencephalon* or *cerebrum*, in many vertebrates handles largely the sense of smell. But the *olfactory lobe* is much reduced in modern birds in consequence of their poorly developed sense of smell. (Some birds, however, seem to use odor in choosing foods.) The sense of taste seems to be well developed in some birds and poor in others.

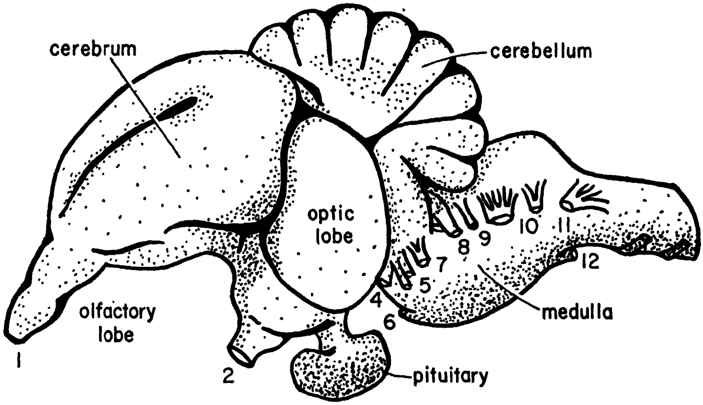

Fig. 4·18. *Brain of the bird (Rock Dove). The numbers indicate the roots of the corresponding cranial nerves. (The third is underneath.)*

The peripheral nervous system consists of *nerves* and *nerve endings* that gather sensory impressions. *Nerve tracts* along which they pass to the central nervous system are sometimes considered as part of the central nervous system and sometimes as part of the peripheral. Nerves connected with the brain are *cranial nerves*, those attached to the spinal cord, *spinal nerves*.

There are twelve pairs of cranial nerves (Figs. 4·18 and 4·19) in birds (a thirteenth, the *nervus terminalis* is probably absent in birds);

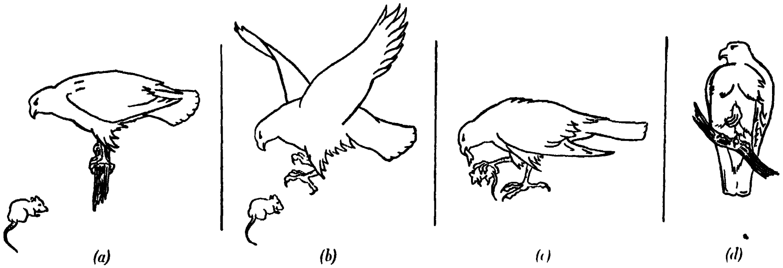

Fig. 4•19. *Function of the cranial nerves (indicated by Roman numerals). (a) Hawk sees rodent, II. (b) Flies to prey: sees rodent, II; focuses eye, III; moves eyes slightly, III, IV. (c) Tears food, V; moves food with tongue, VII; tasting, and salivation, VI, IX; swallows food, X, XII; moves neck, XI. (d) Resting on perch: watches, III, IV, VI; listens, VIII. The olfactory nerve, I, probably plays no part in the feeding process.*

Table 4•5
The Cranial Nerves

Chief Function	Number	Name	Source in Brain	Point of Termination
Smell	I	*Olfactory*	Telencephalon	Olfactory bulb
Vision	II	*Optic*	Diencephalon	Retina of eye
Focusing	III	*Oculomotor*	Mesencephalon	Extrinsic and intrinsic eye muscles
Helps move eye	IV	*Trochlear*	Mesencephalon	Superior oblique eye muscle
Moves jaw	V	*Trigeminal*	Myelencephalon	Jaw muscles
Helps move eye	VI	*Abducens*	Myelencephalon	Lateral rectus muscle
Taste, controls head	VII	*Facial*	Myelencephalon	Taste buds, head muscles, mouth glands
Hearing	VIII	*Auditory*	Myelencephalon	Mouth glands, ear
Control of tongue	IX	*Glossopharyngeal*	Myelencephalon	Pharyngeal muscles
Controls pharynx, syrinx, trachea, esophagus	X	*Vagus*	Myelencephalon	Pharynx, viscera, syrinx
Control of pharynx, neck, heart	XI	*Spinal accessory*	Myelencephalon	Pharynx, viscera
Control of tongue, syrinx	XII	*Hypoglossal*	Myelencephalon	Tongue muscles, syrinx

these nerves are referred to by number. In the course of structural change during evolution of the body, they generally follow the muscle as originally controlled in their ancestors, irrespective of where the muscle may come to rest in modern birds (Table 4·5).

The spinal nerves arise from the spinal cord and are therefore not directly connected to the brain. They are part of a complex organization through which the heart, lungs, digestive tract, blood vessels, and many other parts of the body are controlled "involuntarily." In the bird, the spinal nerves have far greater control over the body than in the mammal. This is illustrated by the rather violent muscular contortions following the simple farmyard practice of decapitating a Chicken. The saying "like a Chicken with its head cut off" in reference to undirected human effort testifies also to the control of the body by the spinal cord in birds.

There are about fifteen to thirty pairs of spinal nerves in the bird. Those in the upper neck region form a *cervical plexus* that innervates the muscles and skin in the head and neck region. Those from the lower neck combine with the first dorsal nerves to innervate the muscles of the wings and breast region through a merger called the *brachial plexus.* The remaining dorsal nerves innervate the nearby region and contribute some innervation to the wings also. The nerves that control the hind limbs and tail region originate in the *lumbosacral plexus* (of three plexi, *lumbar*, *sacral*, and *pudendal*).

Reception of stimuli from the outside is through the sense organs, which in the bird consist chiefly of the ears and eyes. Birds have many nerve endings throughout the skin, however, particularly near the base of many feather follicles. The whole body thus has a sense of touch; in a way, every feather may serve as an "organ of touch."

The bird probably senses in varying degrees the same things humans do, such as heat, cold, pain, hunger, thirst, and kinesthetic senses. The impulse, when picked up by the proper nerve ending, passes to the brain where the actual recognition takes place. Scattered through the muscles and body organs will be found nerve endings for the maintenance of body operations and the reception of internal stimuli, such as feelings of hunger, pressure, muscle position, and the like. Temperature regulation occurs automatically by means of the *thermotaxic nerve* center in the *corpus striatum* of the cerebral hemispheres. Overheating or underheating results in setting in motion appropriate actions for heating (page 86) or cooling (page 87) the body as the need arises. Changes in insulation power of the feather covering play a role in temperature control (Moore, 1951).

Vision. Birds possess very large eyes, often larger than the brain itself (Table 4·3). In fact, the 2-inch eye of the Ostrich is the largest that occurs in any land animal. The eye of a 2- or 3-pound Hawk or Owl, for example, may be as large as or even larger than that of man. A bony *sclerotic ring* (Fig. 4·20) may be present. The rapid accommodation of the eye, perhaps accomplished by moving the lens as in a camera as well as by changing lens shape, necessitates considerable power (Fig. 4·21). A Prairie Falcon, for example, diving at high speed for a small target in the form of a rodent head projecting out of its burrow (page 170) must accommodate rapidly, for mistakes in the bird world are often fatal. So far as known, accommodation is faster in the bird than in other vertebrates.

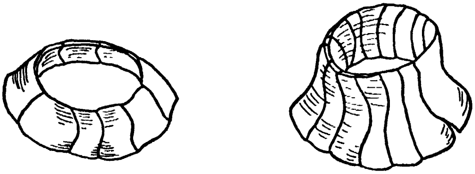

Fig. 4·20. *The sclerotic ring of the Great Horned Owl.*

The retina has great resolving power. In the retinal foveas of a soaring Hawk, a million cones per square millimeter have been reported. The visual acuity of Hawks and Eagles exceeds man's by at least eight times (Walls, 1942). For purposes of adapting eyes to needs of the bird, three chief types occur (Fig. 4·21).

Because the large eye occupies so much of the skull, great muscles would be needed to turn it like the roving eye of man. The bird has simplified matters by having a relatively stationary eye and using the existing neck muscles to turn the head and thereby to accomplish eye motion. In any event, the side position of the eye on the head gives a wide visual area—perhaps three-quarters of a circle (Fig. 4·21).

The eyes of most birds seem to have monocular (one eye at a time) vision to the side, though Owls and some others have both eyes forward for binocular vision. The latter permits special facility in judging distances. It seems evident that birds can judge distance very well and that they are able to adjust from a bill-length focus to an infinite one as rapidly as need be. Most birds have two foveas in each eye, one for looking forward and the other for looking to the side. In the Swifts and Swallows, a third one appears; in Owls there is but one. Because a bird presumably can use but one eye at a time in monocular vision, it appears able to ignore or suppress images in the other eye or another fovea. The temporal foveas, however, give binocular vision in the center of the circle of vision (Fig. 4·21).

Two eyelids, the upper and lower, and a *nictitating membrane* cover the eye. The upper eyelid moves little and a bird usually closes its eye by drawing up the lower lid. The nictitating membrane can be drawn across the eye from its lower nasal position upward and rearward to moisten and clean the cornea. The moisture comes from *lachrymal glands* under the upper eyelids. The *Harderian glands* under the nictitating membrane also supply lubrication.

Nocturnal birds, such as some Owls, have a sensitivity to low light intensities ten to a hundred times greater than that of man. Diurnal Owls, on the other hand, may have no better or have even

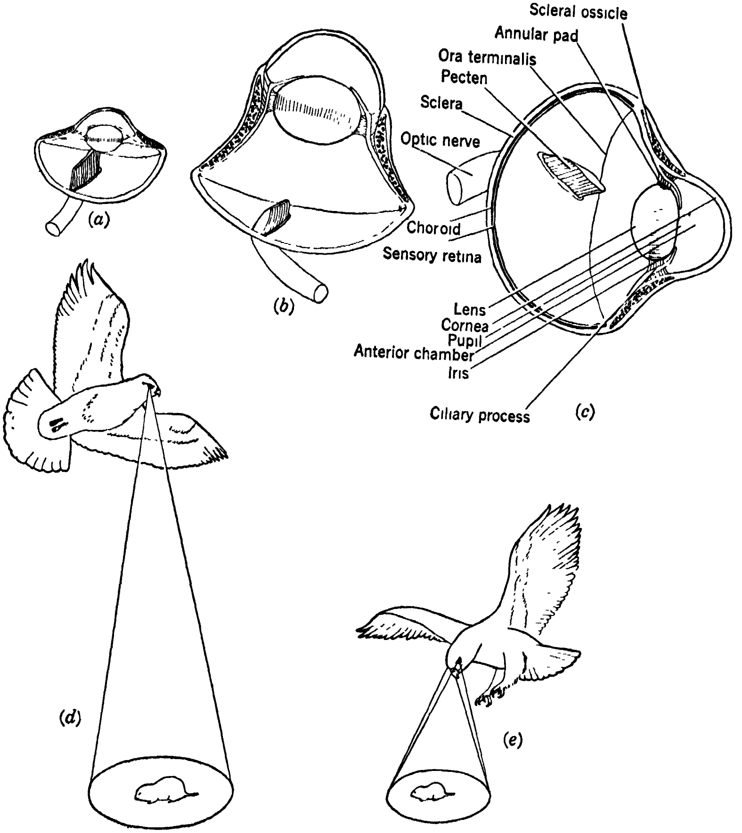

Fig. 4·21. *(a) "Flat" eye common to many birds, (b) "tubular" eye found in Owls, (c) "globose" eye of Red-tailed Hawk with parts labeled, (d) monocular vision through use of the central fovea, (e) binocular vision through use of two temporal foveas. (Prepared by Rex Lord.)*

poorer night vision than man. Under favorable conditions the Barred, Long-eared, and Barn Owls can see to approach prey from a distance of 6 feet or more under an illumination as low as 0.000,000,73 foot-candles (Dice, 1945). This would be the amount of illumination produced by a "standard candle" at a distance of 1,170 feet. Owls may see objects with difficulty down to 0.000,000,15 foot-candles, which would be equivalent to a standard candle at 2,582 feet. The light on a cloudy, moonless night may be 0.000,4 foot-candles, but might fall to 0.000,000,4 on the forest floor in deciduous woods. Hence, prey in the deep shadows of a dark night may not be visible to the best of Owl eyes.

Birds perceive color somewhat as in the human eye, though perhaps with less sensitivity at the blue end of the spectrum and more sensitivity at the red end. The red and yellow *oil droplets* in the *retina* act as color filters. The yellow serves during most of the day and the red in the morning and evening when they are exposed to the *Rayleigh effect* of light scattering. Birds that rise at dawn or earlier, like most Songbirds, have about 20 per cent red droplets; Hawks have about 10 per cent; and Swallows and Swifts, 3 to 5 per cent. Birds that must face the glare over the water have increased numbers of red droplets; thus, the European Kingfisher has 60 per cent, the Water Ouzel (Dipper), 24 per cent; Ducks, 20 per cent; and Herons, 20 per cent. There appears to be no relationship of plumage color and color of oil droplets, save for the fact that green oil droplets have been reported in some green Parrots (Walls, 1942).

Diurnal eyes, such as those found in common daytime birds, are rich in retinal *cones*. These possess red, orange, yellow, and colorless oil droplets. Crepuscular eyes, such as those in the Nighthawk, have a higher ratio of *rods* to cones. They have few or no red and orange droplets, some yellow droplets, but mostly colorless ones. Nocturnal birds have a high ratio of cones to rods for increased visual sensitivity at night, but enough rods are present for good daytime vision. The oil droplets in such birds may be wholly colorless ones.

Hearing. Though the hearing of a bird is relatively good, reaction to sounds may depend much upon sight. Thus, an observer in a blind may make many sounds clearly audible to, but not disturbing to, a bird. Most birds, however, react to sharp sounds whether with or without motion. The hearing range of birds will be discussed further in Chapter 17.

The ear of the bird consists of a middle and inner ear formed of *semicircular canals*, *vestibule*, *tympanum*, *cochlea*, *sacculus*, *utriculus*, and associated nerve tissue (Fig. 4·22). The sound reaches the inner ear through the middle ear by an opening in the skull covered by

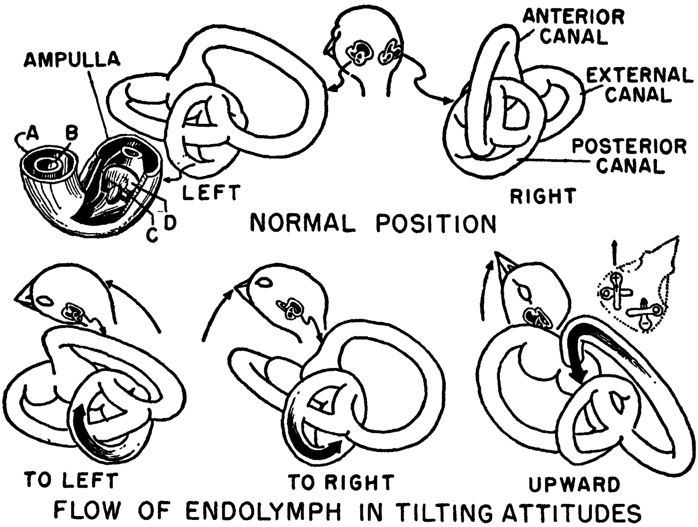

Fig. 4•22. *The semicircular canals maintain balance as in the Towhee* (Pipilo). (*a*) *Bony canal,* (*b*) *membranous canal,* (*c*) *crista acustica,* (*d*) *cupola.* (*From William J. Beecher, "A Possible Navigation Sense in the Ear of Birds,"* American Midland-Naturalist, *46(1951):368.*)

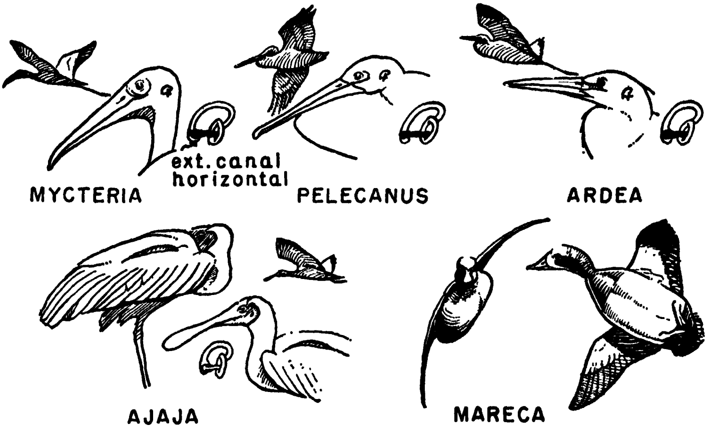

Fig. 4•23. *Normal attitude in birds. The "rest position" is one wherein the external canal is horizontal. Various species attain it in rest or flight by different elevation or depression of the bill. (From William J. Beecher, "A Possible Navigation Sense in the Ear of Birds,"* American Midland-Naturalist, *46(1951):374.*)

special feathers. There is no external ear as in mammals, though an "ear conch" in some birds, particularly Owls, may be an aid to hearing and locating night sounds. The ear conch tends to be larger in Owls of cold climates, apparently an exception to the *Allen rule* (Kelso, 1940; see page 185).

Sounds pass to the tympanum of the middle ear and thence along the rodlike *columella* into the inner ear where as vibrations they are picked up by the hairlike endings of the auditory nerve for transmission as nerve impulses to the auditory center of the brain along the *eighth* cranial nerve.

The ear serves also as the gravity-balancing organ of the body (Fig. 4·23). Equilibrium is maintained by a fluid (*endolymph*) in the *semicircular canals*, which in shifting about stimulates the hair cells. Other parts of the inner ear may participate in detecting movement, such as of changes in speed or direction. A bird in flight or at rest holds its head in a normal position when the balancing organ functions properly. Injury or malfunctioning causes characteristic abnormal behavior. Birds orient themselves to wind in part at least by the balance of air pressure between the two ears.

SUGGESTED READING

BEDDARD, FRANK E., *The Structure and Classification of Birds.* Boston: Longmans, Green & Co., 1898.

BRADLEY, O. C., and TOM GRAHAME, *Structure of the Fowl.* Edinburgh, Scotland: Oliver & Boyd, 1950.

COUES, ELLIOTT, *Key to North American Birds.* Boston: The Page Co., 1912.

FISHER, HARVEY I., "The Occurrence of Vestigial Claws on the Wings of Birds," *American Midland-Naturalist,* 23(1940):234–243.

FISHER, HARVEY I., "Adaptations and Comparative Anatomy of the Locomotive Apparatus of New World Vultures," *American Midland-Naturalist,* 35(1946):545–727

HUDSON, GEORGE ELFORD, "Studies on the Muscles of the Pelvic Appendage of Birds," *American Midland-Naturalist,* 18(1937):100–108.

HYMAN, LIBBIE HENRIETTA, *Comparative Vertebrate Anatomy.* Chicago: University of Chicago Press, 1942.

*NEWTON, ALFRED, *A Dictionary of Birds.* London: Adam & Charles Black, 1893–1896.

QUIRING, DANIEL P., *Functional Anatomy of the Vertebrates.* New York: McGraw-Hill Book Co., Inc., 1950.

SHUFELDT, R. W., *The Myology of the Raven (Corvus corax sinuatus).* New York: The Macmillan Co., 1890.

SHUFELDT, R. W., *Osteology of Birds.* New York State Museum, Bulletin No. 130, 1909.

*THOMSON, J. ARTHUR, *The Biology of Birds.* New York: The Macmillan Co., 1923.

WALLS, G. L., *The Vertebrate Eye.* Bloomfield Hills, Mich.: Cranbrook Institute of Science, 1942.

WEICHERT, CHARLES K., *Anatomy of the Chordates.* New York: McGraw-Hill Book Co., Inc., 1951.

*YOUNG, J. Z., *The Life of the Vertebrates.* Cambridge, England: Clarendon Press, 1950.

5

The Basis of Life

Fundamentally, about all things as we know them, whether those of our own making or those of nature, rest upon transfer of energy at some time or other. Though it may not be visible in man's short time on earth, few things of the universe are so static as not to be part of some energy transfer system. In its way too, the bird is part of an energy transfer process, for the basis of life is the energy liberated in the body cells. In a broad sense, *physiology* deals with the generation and use of energy.

Living things consume energy, and the bird is no exception. Even when a bird is at rest, internal tension, life processes, and temperature demands require energy, and all combine to drain the energy resources of the bird. Living things no doubt differ in their efficiency in using energy, just as man-made machines may differ also. The more efficient users of energy clearly have an advantage over others. As said elsewhere, it is a principle of thermodynamics that when two systems compete in using the same energy resource, the more efficient prospers at the expense of the less efficient. The maximum efficiency of bird muscle is reported to be about 40 to 50 per cent (and possibly more). This compares better than favorably with the 35 to 40 per cent efficiency of diesel engines.

Generating energy to maintain life is the operational role of the "protoplasm" that makes up the animal body. Succinctly speaking, this job of "protoplasm" is just to be alive. "Protoplasm" itself consists of many complex chemical compounds, chief among which are *proteins, fats,* and *carbohydrates*; but more than half, sometimes as much as 90 per cent, is water. In addition, "protoplasm" contains many minerals and other elements (generally in small quantities), such as carbon, oxygen, hydrogen, phosphorus, sulphur, sodium, potassium, calcium, magnesium, chlorine, iron, or copper.

HEAT AND ITS CONTROL

Oxidation. The release of heat and energy results from biological oxidation, either *aerobic* (involving atmospheric oxygen, the usual process of oxidation) or *anaerobic* (involving no atmospheric oxygen). Anaerobic oxidation produces in the body many times the immediate energy of normal oxidation and functions in emergencies. Yet it results in the accumulation of lactic acid and other acids in the muscles. It results also in an "oxygen debt"; hence, it cannot long be sustained without fatigue.

The oxygen used directly in aerobic oxidation and that used indirectly in anaerobic oxidation comes to the tissues chiefly through the *hemoglobin* of the blood. The hemoglobin content of bird blood seems to vary between about 10 and 18 per cent. Diving birds have reserves in the *oxyhemoglobin* and *oxymyoglobin*, so that they are capable of long submergence, though species vary in this capacity (Schorger, 1947). Birds accustomed to high altitudes have a higher erythrocyte concentration than those of lower altitudes, and their blood generally has a higher oxygen affinity. Birds of higher altitudes also have relatively larger hearts (Hartman, 1955). Both the liver and spleen store quantities of blood rich in oxygen that can be put back into circulation. It may be also that birds ascending to high altitudes or diving deep into the water can shift blood from tissues less sensitive to oxygen deficits to the muscles being used or to the nervous system, which is particularly sensitive.

Body Temperature. The normal *diel* (daily) temperature of the *diurnal* bird rises to a maximum in the late afternoon, after which it declines to a low early in the morning. The daily temperature rhythm of *nocturnal* birds (like most Owls) is reversed and reaches its high late at night and its low sometime during the day. Temperature change varies also with activity. Its range varies with size, small birds tending to have a greater variation than large ones. A daily variation of 10.6° F. has been reported for the American Robin, 10.0° F. for the Song Sparrow, but only 1.8° F. for the Domestic Duck.

The average temperature of the female bird usually exceeds that of the male by a small amount, though exceptions have been reported for some species (as among the Ardeidae and Phalaropodidae).

The newly hatched altricial bird is essentially cold-blooded, like its reptilian relatives (Fig. 1·9). Development of temperature control takes some time (Kendeigh, 1939). The newly hatched youngster depends upon brooding by the adult for maintenance of its body temperature, which fluctuates with that of the air when the parent is away. But the body temperature becomes about that of the adult by the time the young leave the nest. In precocial birds, however, temperature regulation is better and the young are more nearly able to maintain normal body temperature. In adults, body temperature may rise and fall with activity and rest but not with hot or cold weather.

Wetmore (1921) summarized findings on the temperature of 327 species of fifty families and added a table of data taken from the literature. Generally speaking, the increase in body temperature from low to high follows the taxonomic position, the more highly placed birds having the higher temperatures. Presumably, the placement of birds reflects somewhat their relative development which in turn would seem to reflect relative efficiency. The higher temperature of the higher-ranked birds would perhaps increase their efficiency as energy consumers. The normal temperature varies from about 103° F. in Grebes and Pelicans to about 109° F. in perching birds (Table 5·1).

Table 5·1

Reported Body Temperatures of Various Species of Birds

Species	Body Temperature	Species	Body Temperature
Cassowary	101.8	Horned Lark	109.4
Kiwi	100.0	American Crow	107.9
Penguin	102.1	American Raven	107.4
Pied-billed Grebe	102.7	Carolina Chickadee	108.0
Albatross	105.2	White-breasted Nuthatch	107.7
Brown Pelican	104.6	Mockingbird	109.2
Canada Goose	106.9	American Robin	109.8
Mallard	106.4	Magnolia Warbler	108.0
Turkey Vulture	103.8	Western Meadowlark	107.6
Avocet	106.6	Cowbird	108.1
Mourning Dove	109.0	Cardinal	109.3
Great Horned Owl	103.8	Chipping Sparrow	107.4
Eastern Nighthawk	106.2	Song Sparrow	109.1
Downy Woodpecker	107.2		

Source: Alexander Wetmore, *A Study of Body Temperature of Birds*, Smithsonian Miscellaneous Collections, Vol. 72, No. 12.

The lowest "normal" temperature seems to be in the Western Grebe (101.3° F.) and the highest in the Western Wood Pewee (112.7° F.). Hummingbirds show low temperatures, but their small size in respect to thermometers may be responsible. Yet it seems that the temperature of the Hummingbird at night drops almost to that of the air as a means of conserving energy resources (Pearson, 1953).

Metabolic Rate. The metabolic rate of birds varies among species; in general, it varies with the two-thirds power of the body weight.

Table 5·2
Body Size as Related to Four Hours of Heat Production
(From various sources)

Species	Body Weight, Grams	Total Calories Produced	Calories per 1,000 Grams	Calories per Square Meter of Surface
"Canary"	16.3	4.9	301	762
"Sparrow"	22.5	5.2	231	652
"Parakeet"	27.7	6.3	227	688
Dove	150	17.2	115	609
Pigeon	278	28.4	102	667
Chicken	2,000	115	55	701
Goose	5,000	272	54	930

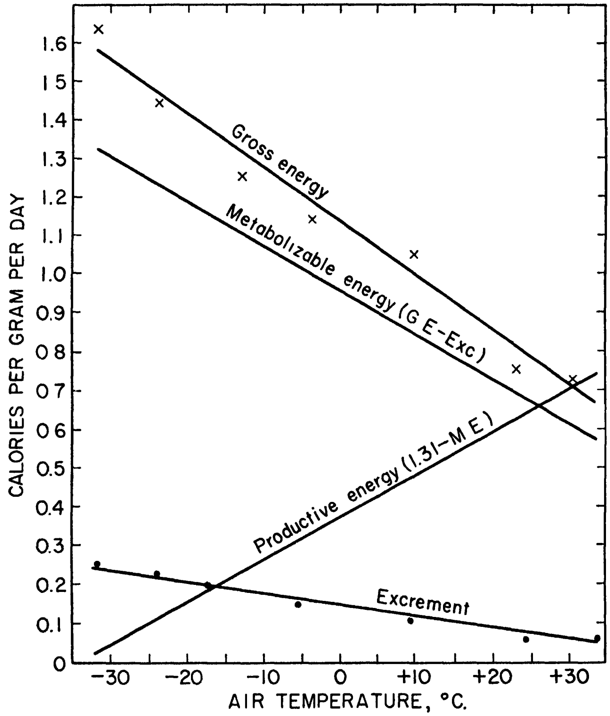

Fig. 5·1. *The energy intake of the House Sparrow increases with decrease in temperature and decreases with increase in temperature. The liberation of productive energy, however, increases with rise in temperature and consequent lower demands on energy of the body for warmth. (After S. Charles Kendeigh, "Effect of Temperature and Season on Energy Resources of the English Sparrow,"* Auk, *66(1949):117.)*

Larger birds thus have a proportionately lower metabolic rate than smaller ones (page 436). In a like manner, a larger bird produces less heat for its body weight than a small one, though the amount produced per unit of surface is about the same, as shown in Table 5·2.

In addition to surface area, it seems probable that shape of the surface influences radiation in accord with Lambert's Law. Perhaps other factors enter into the radiation rate.

It will be seen in the list given (Table 5·2) that though the calories produced per thousand grams of body declined from 301 for the Canary of 16.3 grams weight to 54 for the Goose of 5,000 grams body weight, the calories per square meter of body surface changed relatively little. It was highest (930) for the Goose and lowest (609) for the Dove. The importance of the Bergmann Rule (page 185), as well as its operation, is apparent in the light of reduction of heat produced per unit of weight with size increase.

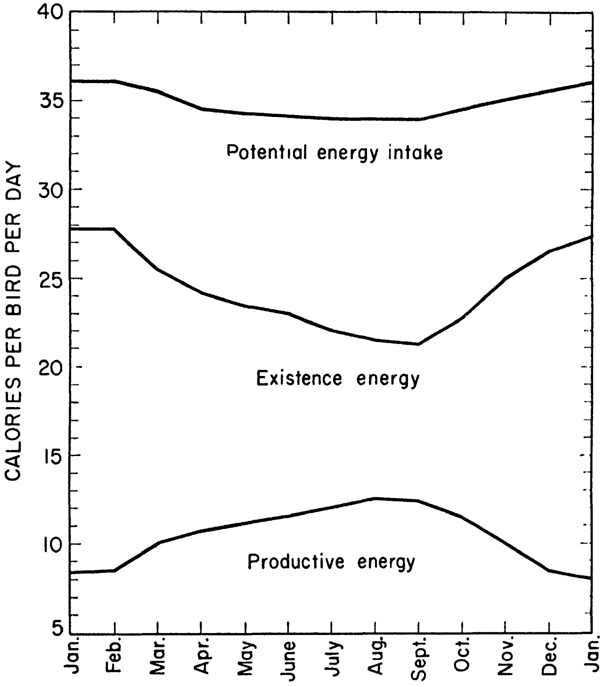

Fig. 5·2. *The energy balance of the House Sparrow varies throughout the year. (After S. Charles Kendeigh, "Effect of Temperature and Season on Energy Resources of the English Sparrow,"* Auk, *66(1949): 113–127.)*

The metabolism of the adult bird increases with decrease of air temperature. More energy from food is needed at low temperatures than at higher ones (Fig. 5·1). The energy required for the House Sparrow at 40° F. below zero is more than triple that required at 100° F. above zero. Just keeping alive at low temperatures obviously is equivalent to a considerable expenditure of energy. At low air temperatures, the body temperature remains normal so long as oxidation can be carried on at high enough rates; failing that, the body temperature declines; if prolonged, it may result in death. Fig. 5·2 illustrates the variations in energy balance of the House Sparrow during the year. At the opposite extreme (high air temperature) the body maintains normal temperature by ventilation and water evaporation in the respiratory system (peripheral circulation in birds is poor). Inability to eliminate heat fast enough means a rise of body temperature and death if prolonged above that normal for the species. Thus both high and low temperatures, if prolonged, may be fatal (Fig. 5·3).

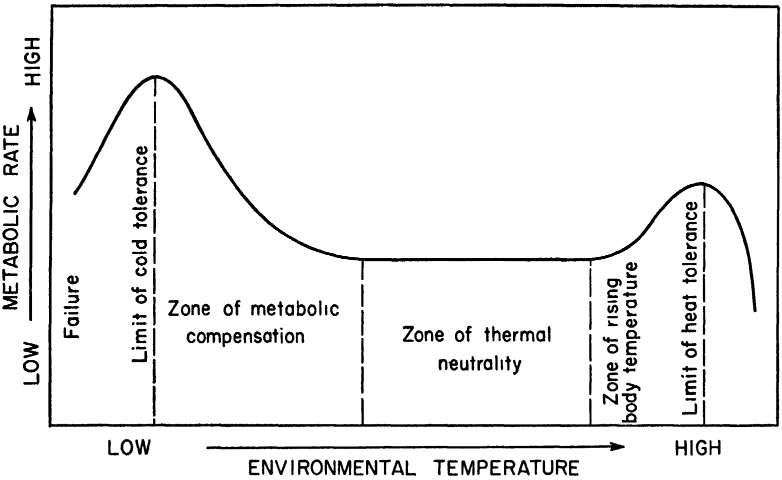
LOW METABOLIC RATE HIGH
Failure
Limit of cold tolerance
Zone of metabolic compensation
Zone of thermal neutrality
Zone of rising body temperature
Limit of heat tolerance
LOW
HIGH
ENVIRONMENTAL TEMPERATURE

Fig. 5·3. *Relationship of the metabolic rate in resting homoiothermous animals to environmental temperatures. (After Douglas H. K. Lee and Ralph W. Phillips, "Assessment of the Adaptability of Livestock to Climatic Stress,"* Journal of Animal Science, *7(1948):391–425.)*

Heart, Respiration Rate, and Cooling. The problem in controlling excess heat is really one of heat dissipation. Birds accomplish this largely by increasing the breathing rate, which at rest on a moderate day may be low but which may rise to 200 per minute at high temperatures. Respiration and heart rates per minute reported for various birds are listed in Table 5·3.

Table 5·3
Heart and Respiration Rates Per Minute

Species	Heart Rate	Respiration Rate
Condor	–	6
Pelican	–	4
"Wild Duck"	185	–
Canary	1,000	100
Chicken	304;312	20;12
Turkey	93	14
Pigeon	244	26
Duck	–	22
Goose	–	16
House Wren	–	112;92
American Robin	–	45
Chipping Sparrow	–	83
Downy Woodpecker	–	131
Falcon	347	–
Hairy Woodpecker	–	120
House Sparrow	800	94;104;140
Blue Jay	–	69;78
Baltimore Oriole	–	107
Starling	–	84
Bronzed Grackle	–	55
Red-shouldered Hawk	–	34
Barred Owl	–	142
Barn Owl	–	184
Great Horned Owl	–	223
Bob-white	322;504;462	64;74,100;142
Ring-necked Pheasant	252;298	44;41;50
Hungarian Partridge	192;264	44;52
Scaled Quail	–	84;170
Plumed Quail	402	89;92

Source: William H. Long, *The Heat Production and Muscular Activity of Two Strains of Wild Turkeys*, Pennsylvania Game Commission, Research Bulletin No. 2.

Under stress of heat, a bird's breathing rate increases—oftentimes to the point of actual visible panting. The Domestic Chicken is reported to have a mean body temperature of 106.2° F. and to show rapid breathing at a body temperature of 107.5° F., panting at 108° F., agitation at 111° F., and gasping at 113° F. We should expect wild birds to have parallel behavior. The breathing rate of the House Sparrow has been reported to be as low as 94 per minute at about 55° F. below zero and 200 per minute at 125° F. above. Some seasonal variation may occur (Fig. 5·4). Panting helps to increase ventilation of the body interior through the lungs and air sacs. At high air tem-

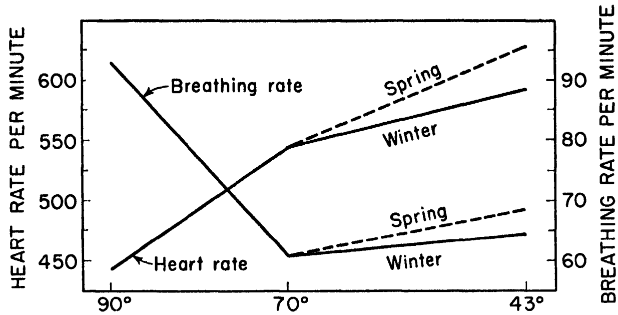

Fig. 5·4. *Average standard heart and breathing rates of the Black-capped Chickadee at air temperatures of 90° F. and 43° F. during winter and spring. (After Eugene P. Odum, "Some Physiological Variations in the Black-capped Chickadee,"* Wilson Bulletin, *55(1943):185.)*

peratures, therefore, most of the heat loss occurs through evaporation, for rapid breathing increases evaporation in the lungs, air sacs, and air passages. It has been suggested that evaporation from the inner surface of the bill pouch while "panting" may aid cooling in the Pelican and Nighthawk (Fig. 5·5). At low temperatures, radiation losses are more important than evaporation losses.

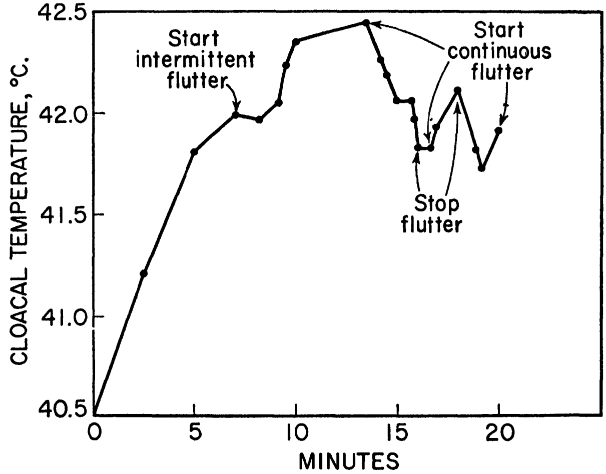

Fig. 5·5. *Effect of gular fluttering on body temperature as measured at the cloaca of a bird placed in the sun. Zero time is the moment when placed in the sun. (After Raymond B. Cowles and William R. Dawson, "A Cooling Mechanism of the Texas Nighthawk,"* Condor, *53 (1951):21.)*

The air temperature at which production needs and radiation needs are neutral (in effect, when the bird feels neither cold nor warm) seems to be about 78° to 86° F. for land birds. Ground inhabitants of the forest and brush have lower *thermo-neutral temperatures* than those of the open, and birds of cooler climates have lower thermo-neutral temperatures than those of warm ones.

Heat Loss. In nature, birds protect themselves against heat loss in a variety of ways. They get into protected areas and fluff up the feathers, for example, which increases the insulation value of the feathers. The bird pulls in its extremities and takes on a humped-up look. Several may huddle together for warmth as well as protection. Homoiothermous animals in general increase body heat by greater muscular activity and by greater outpouring of hormones from the thyroid and adrenal glands to stimulate heat production, as may be seen in Table 5·4. The air temperature, where conservation of heat by insulation becomes insufficient, varies with species. For tropical birds, it seems to be about 20° to 23° C. For the Canada Jay, it may be —10° C. and for the Glaucous Gull —40° C.

Table 5·4

Thermal Response of Endocrine Glands

Gland	Response to cold	Response to heat
Anterior pituitary	Increased thyrotropic hormone	Decreased thyrotropic hormone
Thyroid	Increased thyroxin	Decreased thyroxin
Adrenal medulla	Increased adrenalin	No change unless under great stress
Adrenal cortex	Increased ketosteroids	

Source: Douglas H. K. Lee and Ralph W. Phillips, "Assessment of the Adaptability of Livestock to Climatic Stress," *Journal of Animal Science*, 7(1948):391-425.

OTHER PHYSIOLOGICAL NEEDS AND RESPONSES

Nutrition. Much can be said about the diet of domestic or confined animals, as well as of man himself. But little is known about the physiology of the nutritional aspects of wild birds. On the basis of studies, it seems apparent that the Domestic Chicken, if given a free selection of a wide range of foods encompassing the needs of a balanced diet, will balance its rations satisfactorily. It hardly seems that birds in the wild would do less; but we cannot be sure that birds confronted with a limited dietary (as in winter) will be able to balance their diets with the foods at hand (Chapter 23).

It seems entirely likely that birds, at least many birds, can synthesize sufficient vitamin C for their needs. Other vitamins may be available in adequate amounts in nature during the growing season and perhaps throughout the year. Whether the needed vitamin D, for example, can be carried in the body from summer (when ultraviolet rays penetrate to the bird environment in the North) through the winter (when ultraviolet rays may not reach the surface in the North) is not known for wild birds.

Weight Variations. The weight of the bird may give some indication of its physiological condition (page 401), but we have as yet few standards of comparison (Fig. 5·6). Birds are highly sensitive to environmental influence, and considerable variation occurs among the individuals of a species and between different periods of time for the same individual (Nice, 1938). In general, males are heavier than females, but departures from such a generality may occur. The females of raptorial birds consistently tend to outweigh the males; and young birds that lay on substantial fat deposits may be heavier temporarily than either parent.

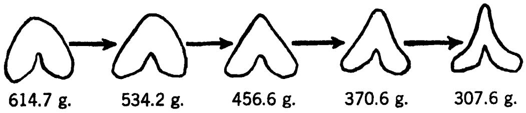

Fig. 5•6. *Breakdown of the body during starvation shows in the reduction of breast muscle in the Coot. The weights in grams of the birds (all males) are shown. (After Milton B. Trautman, William E. Bills, and Edward L. Wickliff, "Winter Losses from Starvation and Exposure of Waterfowl and Upland Game Birds in Ohio and Other Northern States,"* Wilson Bulletin, *51(1939):93.)*

Marked daily (diel) variations in weight may occur. The greatest weight is reached late in the afternoon and the lowest late in the night. The weight will increase or decrease with food intake, as one would properly expect. It varies also with water intake and loss. The diel variation in Passerine birds may reach 12 per cent or more of the mean daily weight. The food eaten probably accounts for much of this, as may be seen in the chapter on food habits, though small birds eat proportionately more than large ones (Fig. 5·7).

Weight may vary seasonally, for short periods, and often with air temperature. Weight loss may be great with a decline of temperature, which probably reflects energy consumption in keeping the body warm. Birds reach their lowest weights generally in midsummer, however, and highest in midwinter or later. Variations in body fat largely account for this.

Among some *migratory species*, the maximum weight is reached immediately before migration in consequence of heavy fat deposition resulting from increased metabolism under the influence of the endocrine system as controlled by the pituitary gland (Wolfson, 1945). This fat deposition can occur with suddenness, perhaps within days but certainly within a fortnight or so, though it may be prolonged for several weeks. It seems evident that the laying on of fat stores energy for migration use, just as a hibernating mammal lays on fat before hibernation. Day length seems to be the controlling factor which induces pituitary changes and fat deposition, not the warming of spring or cooling of fall. But nonmigratory birds, even though of the same subspecies as other populations which migrate, may not lay on fat, even though they are living in the same place and under the same environmental influences. This marks an evident difference in their response to the environment. Female birds take longer for such effects, and lay on fat later, which is in accord with their general practice of migrating later than the males.

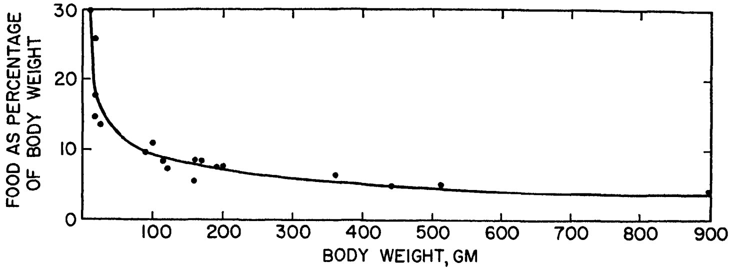

Fig. 5•7. *The relative food intake decreases with increase in weight of the bird. Small birds eat as much as 30 per cent of the body weight daily, while large ones may eat only 3 per cent. (Data after Margaret Morse Nice, "The Biological Significance of Body Weight,"* Bird-Banding, *9(1938):1–11.)*

The increase of day length (*photoperiod*) markedly influences the pituitary, and careful studies demonstrate that light itself influences the pituitary gland after reception through the eye (and possibly to some extent through the skin). Red light has proved most effective and green light the least effective. The stimulated pituitary gland, primarily the *anterior lobe*, in turn stimulates metabolism (as for the production of fat) and particularly the gonads. The gonads increase in size and *spermatogenesis* and *oogenesis* take place with increase in day length. Improper diet may adversely affect the influence of light, though such perhaps occurs infrequently in nature.

Minerals. The bird body needs many minerals, such as calcium for bone growth or egg shells (page 442). Most minerals are needed in small or trace amounts. Field observations indicate that Doves, Crossbills, Pine Grosbeaks, Purple Finches, Evening Grosbeaks, and other species regularly resort to "salt licks." Analysis of several such licks in the West shows that the water-soluble salts present include chlorides, sulphates, hydrocarbonates, and carbonates of sodium. Some magnesium and calcium salts may also be present.

Water Needs. Water needs, like the need for food, play so great a role in the life of birds that their importance should never be out of mind. The water needs of desert birds are particularly pressing, and the gathering of birds at a desert oasis readily testifies to this fact. The sources of water for birds and mammals alike are the same in deserts and humid regions: surface water, dew, succulent vegetation, sap, animal foods, and metabolic water (Vorhies, 1945). In hot climates, much moisture may be needed for cooling the body by evaporation in the lungs, air sacs, and gular membranes.

Many birds drink water at frequent intervals, almost daily in summer for White-winged Doves, Valley Quail, and Turkeys. But many birds of dry habitats clearly have no opportunity to drink. Yet the evident relish with which birds come to water at a feeding station testifies to its attractiveness. Birds on dry range appear to thrive better when moist foods are present, even though they may be able to survive on dry foods. Some may come into breeding condition earlier and more vigorously when an adequate supply of moisture is available.

Most birds drink by dipping the bill in the water, elevating the head, and allowing it to run down the throat, but Doves drink without raising the head.

Marine birds often have no opportunity for obtaining fresh water for long periods of time. Some birds very clearly drink sea water, but others are made ill by it. The Adélie Penguin, for example, during the period of courtship ashore in the Antarctic spring, eats snow, a water form nearly as pure as distilled water. Yet later it drinks salt-laden sea water. Gulls, Waterfowl, and many other birds seem able to use both fresh and salt water. The salt-secreting ability of the kidneys appears particularly good in marine birds using sea water, but of this we are woefully ignorant (Murphy, 1936).

Humidity. Atmospheric humidity influences the physiological well-being of birds, especially during hot weather. For some, the high humidity may well be a part of the environment to which they have become adjusted. But others, particularly in the mid-latitudes where most people interested in birds live, may not have become completely adjusted to high humidity. In hot weather, it retards evaporation and the consequent cooling of the body. In cold weather, it increases the conductivity of air and thereby the loss of heat. Paradoxical though it may seem, high humidity may be unfavorable in both hot and cold weather.

The egg also requires a rather fixed humidity for best development of the embryo. A humidity greater than 50 per cent may be less favorable than a lower one; it may be harmful. Low humidity, on the other hand, may cause excessive drying of the egg and may also cause some metabolic distress in the embryo. The eggs of water birds generally require a higher humidity for hatching successfully than do those of land birds.

Sleep. The physiological relaxation attendant upon sleep is little known for birds except in a most general way. The temperature, heart rate, and respiratory rate drop with night-time inactivity. But the mitotic rate, which measures the rate of repair or growth, increases. The eyes probably serve as the means through which darkness influences the body. Bodily fatigue also probably acts in coordination with the eyes and with other organs. Some birds seem so lacking in nervous response on their roosts as to be almost unaware of sounds and other disturbances (Fig. 11·3). Others seem rather easily disturbed.

MAINTENANCE OF LIFE

Starvation. Differences in survival time of starving birds may in part account for the inability of many birds to remain through the northern winter, though this may in itself be correlated with their life habit of absenting themselves from cold country in winter. As a general principle, well-fed birds are immune from normal adverse effects of cold in their native range. But a bird insufficiently fed, one with insufficient bodily reserves, or one unduly exposed may not be able to survive cold for any length of time. Thus, a bird going to a cold roost on an empty stomach may perish if the air temperature falls. Nine to 14 hours may be the maximum survival time at low temperature for a common migratory Passerine bird with an empty stomach. Hence, the northward wintering of many birds becomes impossible during the long nights and short days of winter in higher latitudes.

The ability to withstand cold nights, especially when hungry, varies among species and individuals (Kendeigh, 1945c). To survive at low winter temperatures, most small birds must feed daily not only to supply energy used during the day but also to restore energy used the night before and to lay up energy for the night to come. In addition, resident and wintering species in cold regions are better able to withstand such stresses than are migrants that move out. Thus the Slate-colored Junco and Tree Sparrow are better able to survive cold and hunger than the White-throated and White-crowned Sparrows. Conversely, the more southerly birds can survive higher summer temperatures better than can northern and Arctic ones.

It seems well established that the flock roosting habit of the Bob-white covey (in a circle on the ground) has a survival value. A depleted covey is reported unable to survive cold night temperatures so well as a normal covey of a dozen birds, which may be a factor partly helping to explain why depleted coveys merge with others. The Bob-white covey in the North averages about two birds more than the covey of the South, evidently as an adjustment to greater cold of the North (page 239).

Survival. All of a bird's energy is derived from the food it eats. To keep alive, the body must have a flow of energy from the outside. Interruption of this flow means that the body must call upon stored reserves, which it consumes until death ends the process. Experimental exposure to temperatures lower than usual for the species indicates that survival time for the House Sparrow without food declines at the rate of one-half hour for each two degrees of drop in temperature (Kendeigh, 1945, 1949). The presence of fat and other stored resources increases resistance. Also, the larger and more robust the bird, the longer the survival time under starvation. The Turkey, for example, is about fifty times larger than the Bob-white, and its survival time is about five times as long. The Bob-white in turn is about six times the size of the White-crowned Sparrow and has a reported survival time of about three times as long. But there are no doubt many differences among species, just as there are among individuals. These differences may result from differing amounts of stored fat and other energy sources and the rate at which they are utilized.

Of 136 House Sparrows picked up after a severe storm, 72 revived and 64 perished. In body measurements, those that perished varied most from the average of the type. It has therefore been suggested that those individuals which depart most from the average (which may be the "ideal" for the species) are most vulnerable to destruction when conditions become unfavorable (Bumpus, 1899). It has been shown, however, that in a large series of birds of the same sex and species, a natural variation of 15 to 20 per cent occurs in general size. Parts of the body may even vary independently of each other in a range of 15 to 20 per cent.

SUGGESTED READING

BALDWIN, S. PRENTISS, and S. CHARLES KENDEIGH, *Physiology of the Temperature of Birds*. Science Publications, Cleveland Museum of Natural History, 3(1932).

BALDWIN, S. PRENTISS, and S. CHARLES KENDEIGH, "Variations in Weight of Birds," *Auk*, 55(1938):416–467.

BISSONNETTE, THOMAS HUME, "Experimental Control of Sexual Photo-Periodicity in Animals and Possible Application to Wild-Life Management," *Journal of Wildlife Management*, 2(1938):104–118.

BRODY, SAMUEL, *Bioenergetics and Growth*. New York: Reinhold Publishing Corp., 1945.

GERSTELL, RICHARD, and WILLIAM H. LONG, *Physiological Variations in Wild Turkeys and Their Significance in Management*. Pennsylvania Game Commission, Research Bulletin No. 2, 1939.

KENDEIGH, S. CHARLES, *The Role of Environment in the Life of the Birds*. Ecological Monographs, 4(1934):299–417.

PROSSER, C. LADD (ed.), *Comparative Animal Physiology*. Philadelphia: W. B. Saunders Co., 1950.

STURKIE, PAUL D., *Avian Physiology*. Ithaca, N. Y.: Comstock Publishing Assoc., 1954.

WETMORE, ALEXANDER, *A Study of the Body Temperature of Birds*. Smithsonian Miscellaneous Collections, 72(1921): No. 12.

WOLFSON, ALBERT, "The Role of the Pituitary, Fat Deposition, and Body Weight in Bird Migration," *Condor*, 47(1945):95–127.

WOLFSON, ALBERT, "Day Length, Migration, and Breeding Cycle in Birds," *Scientific Monthly*, 74(1952):191–200.

6

Egg and Embryo

Reproduction in birds depends upon the satisfactory performance of the *reproductive system* (*genital system*) and body functions associated with breeding. The major associated functions (including breeding behavior) will be treated in their appropriate places, particularly in Chapters 18 and 19. This chapter will therefore be devoted largely to the subject of egg production and development before hatching.

THE REPRODUCTIVE SYSTEM

Gonads. The genital system of birds consists of *gonads* (*testes* in males and *ovaries* in females) and ducts for transfer of the *ova* and *spermatozoa* to the outside (Fig. 6·1).

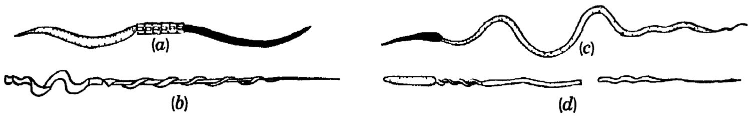

Fig. 6·1. *Examples of avian sperm.* (*a*) *Domestic Chicken,* (*b*) *Tyrant Flycatcher,* (*c*) *Domestic Pigeon, and* (*d*) *Sheldrake.*

Male. The testes of the male are paired organs producing the spermatozoa. The right testis may bulk larger than the left, which itself may be longer and narrower than the right one. During the breeding season, the testes expand in size, often many times larger than when quiescent during the nonbreeding season. The expansion occurs in the testicular tissue, in the number, size, and development of the *spermatogonia,* and in the interstitial cells. These latter cells function as the endocrine portion of the testes and produce *testos-*

terone, which governs the manifestations and behavior associated with sex and reproduction.

Spermatozoa develop in the *seminiferous tubules* and pass from the testes through *efferent ducts* to the *epididymis*, and from that to the *sperm duct* (*vas deferens*), through which they pass to the *cloaca.* In some breeding Passerines, the cloaca bulges out in a *cloacal protuberance* owing to development of the *seminal glomera.* Near the cloacal end of each sperm duct, an enlargement forms the *seminal vesicle,* which stores sperm and produces secretions for carrying them (Fig. 6·2).

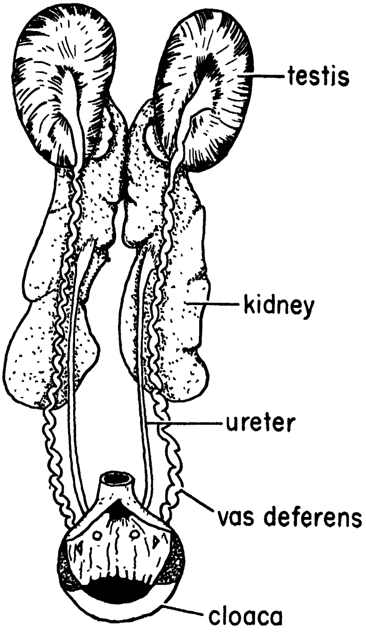

Fig. 6·2. *The male urogenital system consists of the testes (the right one is on the left in the picture) and associated structures for transfer of the spermatozoa to the outside.*

Female. The gonads of the female (Fig. 6·3) begin in the early embryo as paired ovaries, but the *right* fails to develop so that only the left ovary becomes functional. In some members of Falconiformes (perhaps a half or more of all individuals), the right ovary persists, but it is not usually functional. The same occurs also in some Ducks and a few other species, and perhaps 5 per cent of common birds have a vestige of the right ovary. (A few cases have been reported of Domestic Chickens and Ducks with both ovaries and both oviducts functional.) The right *oviduct* dwindles in accord with its ovary. The retention of but a single ovary no doubt evolved as part of the process of weight reduction for an aerial life. The fact that one testis in the male is smaller than the other, sometimes markedly so, suggests a possible trend in the same direction in the male, though perhaps not so rapid as in the female because of the already small size of the testes themselves. This difference may, however, be merely lack of symmetry, for a similar difference occurs in other animals.

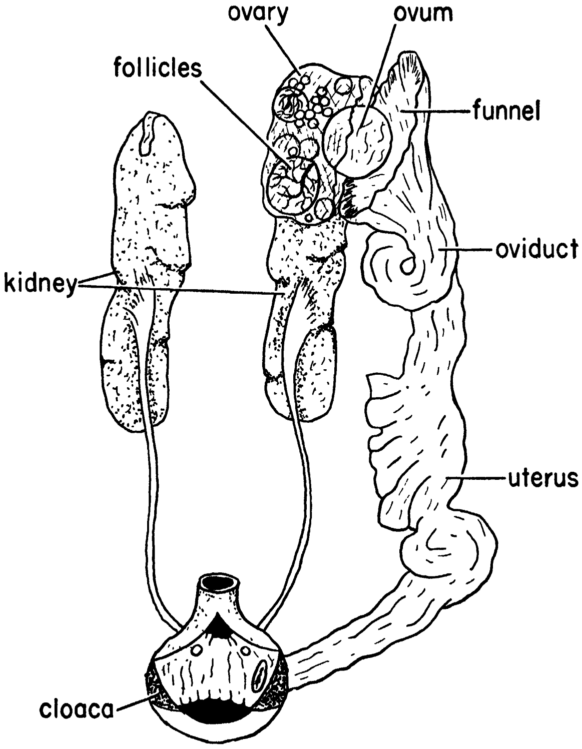

Fig. 6·3. *Reproductive organs of the Domestic Chicken. A portion of the oviduct has been cut away to show a descending ovum.*

Breeding Rhythm. The gonads increase in size seasonally in preparation for the reproductive period. The increased length of daylight in late winter in the middle and higher latitudes evidently stimulates the pituitary to release *gonadotropins* in sufficient amount to bring the bird into full breeding condition. These *gonadotropic hormones* act upon the interstitial cells of the gonads, which elaborate the respective hormones, *testosterone* (male) and *esterone* or *estrogen* (female).

Following the breeding season (usually during the shortening of day length), a marked regression takes place in the gonads, along with all the dependent reproductive activities and conditions. It may be that the hormone *prolactin* plays a part in blocking the action or release of gonadotropic hormones of the pituitary so that light no longer influences the reproductive cycle. This condition (sometimes called *refractory period*) wears off or otherwise terminates by the following spring. In the fall, sporadic activity similar to the breeding season (*fall recrudesence*) may occur in some species. The whole subject of breeding rhythm, light, and endocrines, however, is one of intensive study and some conflicting conclusions.

Fertilization. The spermatozoa pass into the cloaca from which they are transferred to that of the female by direct contact during copulation (page 356). The spermatozoa propel themselves up the oviduct from the cloaca by means of their motile tails. The length of time they take is not entirely known, though it may be relatively short. The duration of viability in the oviduct varies; it may be as much as two months in the Gentoo Penguin (page 356). Fertilization usually takes place at the upper end of the oviduct.*

THE EGG

Initial Growth. The ovum enlarges rapidly as a result of accumulations, largely protein and fatty acids, from the blood stream. It may increase by as much as twenty-five times the original volume in the first 24 hours. It passes out of the ovary into the body cavity where it is picked up by the adjacent *funnel* of the oviduct. The *albumen* and *shell* are laid down in the oviduct, though the *yolk* and *vitelline membrane* are laid down in the ovary. The yolk, albumen, and shell comprise about 53, 35, and 12 per cent, respectively, of the egg in precocial birds and 73, 20, and 7 per cent in altricial birds (Romanoff and Romanoff, 1949).

The cells of the embryo begin to divide shortly after fertilization and continue to do so in the warm environment as the egg travels down the oviduct. Albumen is added by glands, followed by a thin membrane, and finally the hard, limey shell. Mechanical passage of the egg mass down the oviduct seems sufficient to stimulate the glands into activity, although chemical stimulators may be present.

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* No cases of parthenogenesis are known in nature, but experimental incubation of unfertilized eggs of the Domestic Turkey showed development of embryos in 14.1 to 22.4 per cent (*Science*, 1954, 120:545-546).

Egg Shape. The shape of the bird egg varies from nearly spherical to relatively cylindrical (Fig. 6·4). But the commonest shape is

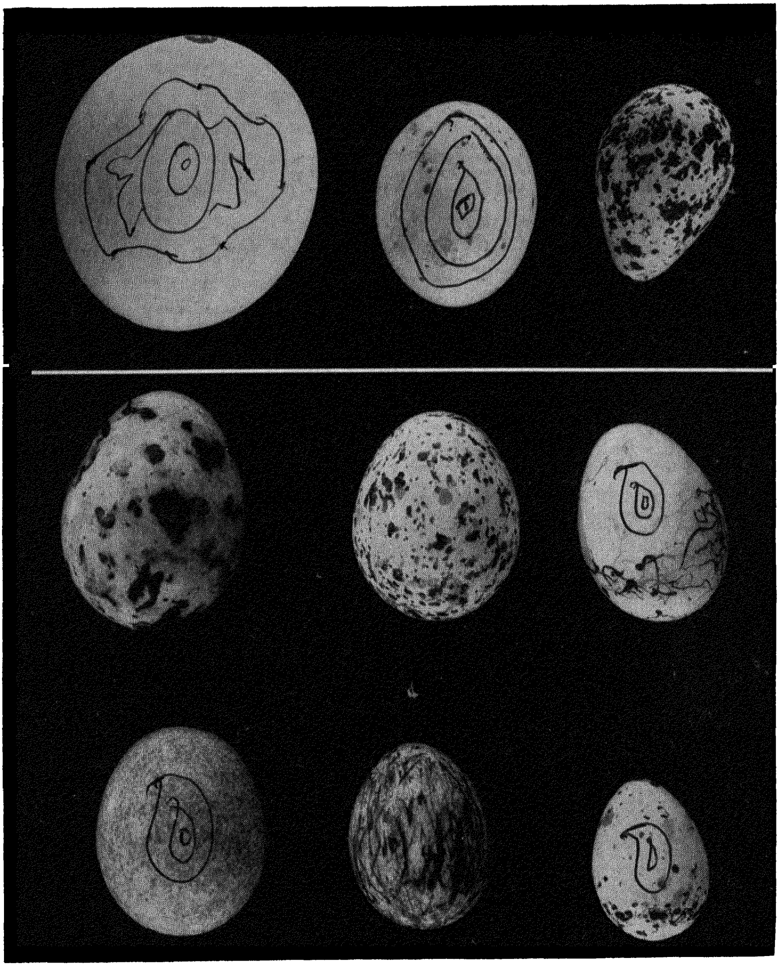


Fig. 6·4. *The shape of bird eggs varies from nearly spherical to sharply acute and the color from unmarked white to richly colored and marked. Top: Horned Owl, Killdeer, and King Rail. Bottom: (upper row) Bronzed Grackle, Blue Jay, Baltimore Oriole; (lower row) Brown Thrasher, Ash-throated Flycatcher, Orchard Oriole.*

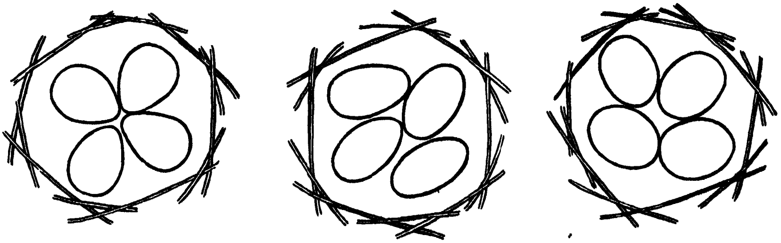


Fig. 6·5. *Diagrams showing the closer fit of acute eggs (left) than long (center) or elliptical (right) ones.*

of an ovoid type in which one end is large and the other pointed. Bird eggs are rather varied in shape, actually; eggs of the Grebe, for example, are pointed on both ends, and the eggs of many Shorebirds and cliff nesters have the pointed end acute. The latter shape may have some survival value in cliff nesters as the egg rolls in a short circle, if disturbed, instead of off the ledge. The acute (or pie-shaped) eggs of Shorebirds and other small birds which lay a disproportionately large egg fit more closely together and permit the small body to cover a greater mass of eggs than would otherwise be the case (Fig. 6·5).

Egg Passage. Two sets of muscles in the oviducal walls cause the egg to progress. The outer, longitudinal ones shorten the oviduct by contraction; the inner, circular muscles reduce the bore. Coordination between the two sets of muscles and variations in tension ahead and behind the egg mass move it forward and shape it. Eggs with large amounts of albumen and yolk are likely to be elongated, while those with small amounts will be rounded. In the Domestic Hen, and probably other birds, the egg is reported to move pointed end first (Romanoff and Romanoff, 1949).

Egg Surface. The surface texture of the egg shell results from the molding effect of the oviduct lining. Rough linings give pitted sur-

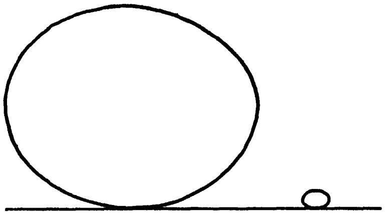


Fig. 6·6. *The egg of the Ostrich compared to that of the Ruby-throated Hummingbird. The surface of many Ostrich eggs bears heavy pits.*

faces and smooth linings, smooth surfaces. The eggs of Woodpeckers are smooth and glossy; those of the Tinamou are highly polished and porcelain-like. Heavy pitting occurs in the shells of many Ostrich eggs (Fig. 6·6) and lesser pitting in those of some Grebes.

Egg Color. Glands in the wall of the oviduct secrete color in the form of pigment drops, especially in the lower end of the oviduct. Uniform color may result from color deposited in the shell material itself or in the last thin layer to be applied. If examined carefully, the egg shell may appear layered, sometimes in layers of different color. Different glands in different parts of the oviduct lay down the several layers. Usually only the final, outside layer of shell carries the color, but inner layers may sometimes be colored.

The egg of the Ani (*Crotophaga*) appears white on account of a chalky outer layer that can be rubbed or scraped off easily to reveal a greenish or bluish undercolor. Clearly, the final layer put on is white. In some birds the outer color is blue, in others it is green. But the commonest color seems to be light shades of brown, such as pale buff or cream. Blue eggs are perhaps next most common and green colors are rather uncommon. Other colors have been recorded at times. The Loon egg is a dark brown; the egg of the Emu is so dark a gray as to appear black. No red eggs are known, though some rich brown ones have been reported. It is said that the least protectively colored eggs are the most palatable to mammals (Cott, 1952).

Markings. The pattern or shape of markings on shells not uniformly colored vary with the species and individuals or even between eggs of the same bird, although all eggs of the same bird tend to be similar (Fig. 6·4). The markings usually are brownish or red-brown, secreted through the openings in the oviduct. If the pigment sets rapidly, the markings will be spotted or slightly linear. But if the pigment sets slowly or its secretion is prolonged, the markings will form streaks. The markings may be smeared or even form blotches if the egg moves much. If the egg rotates in the oviduct, the result will be spiral markings.

Some aberrant changes in marking, such as streaks overlaid with a plain color, can be attributed to unusual happenings in the oviduct. Among these appears to be a reversal of peristalsis in the oviduct to cause the egg to reverse direction at some stage. This reversal may also cause the reversed egg to be enclosed within another shell, as well as other reported abnormalities.

Egg Color and Life Habits. Birds that nest in holes, like Owls and Woodpeckers, lay white eggs. Doves also lay white eggs, as does the Whip-poor-will. Although the white egg of hole-nesting birds has popularly been attributed to the lack of need for protective coloration in the security of a cavity nest, a better explanation perhaps is that the white color enables the incubating bird to discern the eggs better in the dim light of the cavity. The fact that Whip-poor-will eggs are white and that the bird feeds only after dark may involve the same explanation. Eggs of the Nighthawk, on the other hand, are streaked. Nighthawks feed by day or at twilight and do not need the greater visibility occasioned by white eggs. The eggs of a Nighthawk are exposed more in daylight also.

The use of the markings seems associated with protective coloration. In some birds, particularly the Shorebirds and the Nighthawk, the eggs so closely resemble the background as to be scarcely visible, even to an observer at close range. The eggs of the Killdeer blend into the background of pebbles which the bird gathers together at the nest. It suggests that the gathering of pebbles marks an instinctive act associated with the egg pattern to increase possibilities for survival.

Birds that lay eggs covered by streaks usually build nests lined with dry grass or other vegetative material which carries out the linear appearance of the egg pattern. Birds that use mud, feathers, sticks, or leaves for the nest lining tend to lay plain eggs or eggs having blotches of color rather than streaks. But there are many exceptions to any general rule, some of which can be accounted for on the basis of our knowledge of bird life but others cannot. Some may represent inborn traits reflecting habits of an earlier period in the history of the species. Thus, most of the hole-nesting birds lay plain, white eggs, but members of the Wren family lay speckled eggs in the hole nest. The Wrens probably took up hole nesting only recently, phylogenetically speaking, and have not yet lost the tendency for color pattern in the eggs. The Bluebird still constructs a thrushlike nest in a hole where it lays blue eggs. It is presumed to have become a hole-nester in recent Bluebird history. Hole-nesters of presumably long standing do not build a nest in the cavity but lay eggs on the cavity floor. Construction of a nest in a hole (really a rather unnecessary use of energy) is suggested as evidence testifying to the recency of the hole-nesting habit on the part of a bird whose construction instincts are still those of a bird which does not nest in holes.

In general, the external appearance of the bird egg varies because of hereditary, physiological, anatomical, and environmental factors. The fact that the eggs of a species tend to be similar for all individuals testifies to the overpowering influence of heredity. Even the variations in the eggs of an individual bird are likely to be about the same for all its eggs, those of the same set and season as well as those of later years of reproduction.

Egg Size. The size of the oviduct determines the diameter of the egg, which varies in general with the size of the bird. Obviously, the larger the bird, the larger should be the expected egg and embryo, but larger birds lay relatively smaller eggs than do smaller birds. Eggs have been reported to increase in size with the 0.73 power of the body weight. Many exceptions occur in nature, and some groups have peculiarities all their own. Precocial birds need more food for embryonic development and a larger reserve at hatching, which the albumen and yolk provide, respectively. The size of the Shorebird egg is particularly noteworthy for its large size in proportion to the bird body. It may be as much as ten times the size of eggs of similar-size Passerines (Fig. 6·7). The Ostrich has the largest egg of all living birds and the Hummingbird the smallest (Fig. 6·6). The egg of the extinct Elephant Bird (*Aepyornis*) of Madagascar reached a record, 2-gallon size.

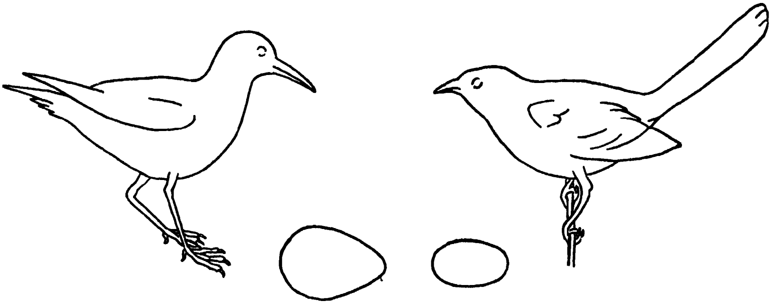


Fig. 6·7. *The egg of the Shorebird on the left is much larger than that of the Passerine bird of the same weight on the right.*

The long axis varies more than the short axis in eggs for the evident mechanical reason that the distensibility of the oviduct is limited. The ratio of diameter to length increases in migratory birds as compared to semimigratory or resident ones (Averill, 1923), a variation accomplished sometimes by reduction in the bore of the oviduct (in line with general reduction of visceral parts in migratory birds or birds of powerful flight) and sometimes by increase in egg volume.

Egg Weight. The weight of the egg in proportion to the size of the bird declines as the body weight increases, though this may not be the case for many of the Fringillidae (Amadon, 1943). The egg weight may exceed 10 per cent of the body weight in small birds but be less than 2 per cent in large ones. The egg of the Kiwi weighs 400 grams or more, which is about a sixth to a fourth of the body weight of 2,500 grams and holds the record for relative size (Fig. 6·8). The birds parasitized by the Old World Cuckoo are smaller than the Cuckoo, but the latter lays an egg about the size of the host egg, a characteristic assumed to reflect an adaptation to laying in the nest of small birds (Chapter 13). In this case, the egg of the Cuckoo is about 3 per cent of the body weight instead of 10 per cent as in the host. Though there are variations in size of eggs within the species and among eggs laid by the same bird, the eggs of each species and of each individual have a general uniformity. First-year females usually lay smaller eggs than more mature ones. (But the size of the egg declines during "old age" in Domestic Chickens.) The larger eggs of mature birds perhaps result from stretching or relaxing of the oviduct.

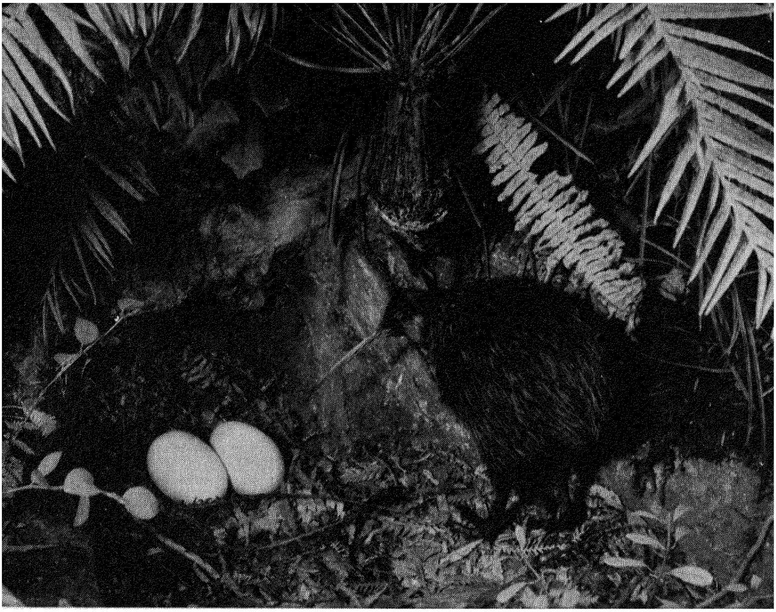


Fig. 6·8. *The Kiwi lays the largest egg for the body size of all birds; it may be about a sixth or more of the body weight.* (*Courtesy of Chicago Natural History Museum.*)

Because bird eggs have a specific gravity of but slightly more than water, the weight in grams gives a rough figure also of the size in cubic centimeters. The volume has also been stated to be about one-half the product of the length times the squared diameter, although the shape of the egg will materially influence this.

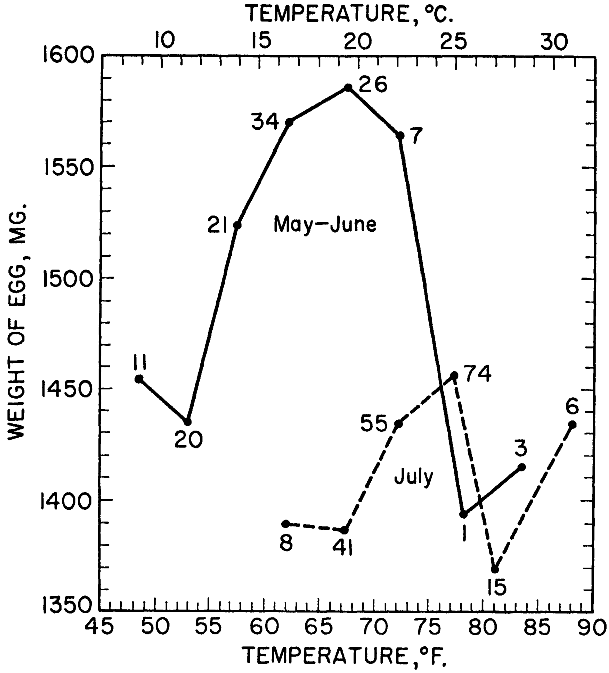


Fig. 6·9. *Weight of newly laid House Wren eggs correlated with the average temperature for three days preceding laying. The number of egg weights is indicated for the respective points. (After S. Charles Kendeigh, "Length of Day and Energy Requirements for Gonad Development and Egg-Laying in Birds,"* Ecology, *22(1941):245.)*

Table 6·1

Some Eggs of Like Incubation Periods

Species	State at Hatching	Egg Weight in Grams	Incubation Period in Days
Emu	Precocial	600	56
Diving Petrel	Altricial	15	56
Ostrich	Precocial	1,500	42
Puffin	Altricial	60	42
Mute Swan	Precocial	350	35
Black Swan	Precocial	290	35
Stock Dove	Altricial	16	16–18
Broad-tailed Hummingbird	Altricial	0.5	16
Flicker	Altricial	7.8	11–12
Cowbird	Altricial	3.2	11–12

Source: Margaret Morse Nice, "Problems of Incubation Periods in North American Birds," *Condor* 56(1954):173–197.

The average weight of eggs and the number per clutch may decline as the season advances. High air temperature may have an unfavorable influence upon the size of eggs as well as on the number laid (Fig. 6·9). Table 6·1 shows a few examples of the size range of bird eggs and incubation periods for a few species.

Number of Eggs. The number of eggs laid by a bird varies with the species, as has been said earlier. In general, it varies within fixed limits, but in some birds the number is definite. The Passenger Pigeon lays but a single egg, and the Band-tailed Pigeon also lays one. Other birds that lay but a single egg are the California Murre, Rhinoceros Auklet, Tufted Puffin, Petrels, and some of the Penguins. The California Condor not only lays a single egg but is believed to lay every other year or perhaps at even longer intervals.

The number of eggs that a bird may be capable of laying seems to exceed the actual number laid in most species, probably as an adjustment for potential egg losses (Chapter 14). The Ruffed Grouse lays at most from 9 to 15 eggs in a set and the Bob-white 12 to 20, but removal of eggs so as to leave but one or two has resulted in a Grouse laying 36 and a Bob-white 128 before stopping. A Yellow-shafted Flicker similarly treated laid 71 eggs in 72 days. Other large numbers laid have been: Wryneck 48, House Sparrow 51, Mallard Duck 146 (in 158 days). The Jungle Fowl normally lays a set of 11 to 14, but one once laid 361 and another 309 before stopping. The Turkey has laid as many as 100, and a caged Canary 60. The reverse experiment, that of adding eggs to the nest, may have the opposite effect. If a bird has laid but one or two eggs in a nest, artificial addition of enough to complete the set may result in the bird's laying fewer eggs. Birds affected by adding or subtracting eggs in the nest have an *indeterminant* type of laying; those not affected have a *determinant* type. Application of stringent standards indicates that perhaps few birds are really indeterminant layers (Davis, 1955).

The amount of mineral and nutrient material in the body is limited, so that a bird cannot lay indefinitely without replenishing its supply. In the case of the Domestic Hen, experiments indicate that not more than an 11-day supply of calcium can be stored in the body. The phosphorus supply has been enough to last 107 days on a phosphate-free diet.

The greatest egg-laying effort for the Domestic Hen (admittedly not a good example for comparison) seems to be a record of 1,515 eggs laid in eight years, but the record will probably fall soon. It is likely that birds have sufficient body capacity to lay all eggs necessary for normal production to maintain the respective species under ordinary conditions to be expected in the wild.

Laying Time. *Ovulation* in most small birds seems to occur at intervals of about 24 hours. It may recur within a few minutes after an egg has been laid. The time needed for the actual process of laying an egg varies from a matter of seconds sometimes in socially parasitic birds like the Cowbird (pages 235, 369) to perhaps 1 to 2 hours in Turkeys and Geese. The Bob-white has been timed and needs but 3 to 10 minutes at the nest to deposit an egg. Most small birds may require about the same length of time.

THE EMBRYO

Early Embryonic Development. Embryological development long has been studied in the abundant supply of developing Chicken eggs, so that the embryology of the Chicken, especially in the early stages, is well-known, standard zoological demonstration material (Figs. 6·10, 6·11).

Development begins even at the moment of fertilization and continues in the egg so long as conditions are favorable. Rapid development occurs as the egg passes down the oviduct where temperature is optimum. Because an egg takes several hours to pass (it varies from a few hours to twenty-four or perhaps more), the embryo may be

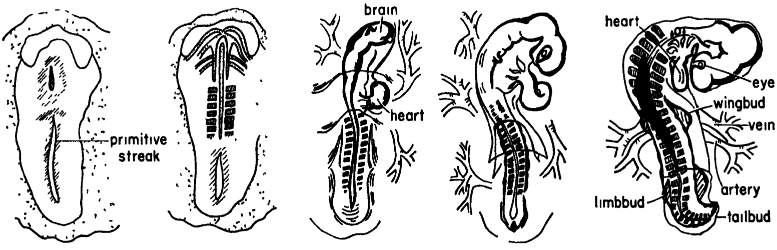


Fig. 6·10. *The chick embryo during its first 72 hours of development.*

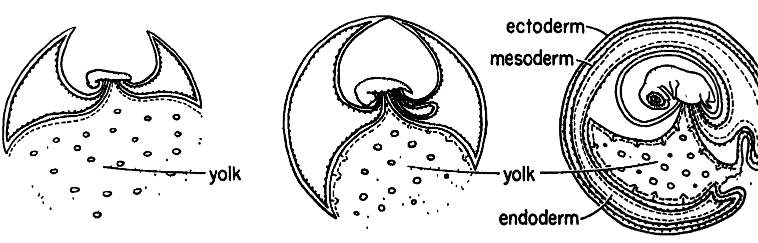


Fig. 6·11. *Three stages in development of the chick and the embryonic layers.*

several hours developed by laying time. In the Chicken egg, the embryo reaches the primitive-streak stage when laid. Fig. 6·12 shows the structure of a fertile egg.

Incubation Rate. The incubation rate varies with the heat supplied by the incubating bird. It slows up (or even ceases) when the bird leaves the nest (page 371) and resumes after heat again reaches the embryo. It cannot be shortened by exposure to high temperature. Development ceases altogether below about 80° F. (21° C.). Yet the cooling periods attending the departure of the incubating bird actually may stimulate development of the embryo and thereby compensate for lowered temperatures (Kendeigh, 1940). Incubation may be suspended for some time without injury to the embryo. In the case of a newly laid egg, because embryonic development started at fertilization, this suspension may be for 3 weeks or even more in Bob-white and other birds laying large numbers of eggs. It may be for only a few days in the average Passerine bird or not at all in birds like the American Cuckoos that start incubation with the first egg. (In the last-named case, the first-laid egg hatches several days before the last one; the size of the young varies correspondingly.) The body temperature of the embryo and nestling fluctuates with incubation and brooding by the parents.

Air temperature during the suspension period may adversely affect the hatchability of the newly laid eggs. Birds native to warm regions lay eggs that can stand high air temperatures (some of which may reach the nineties at mid-day) and still hatch well. But eggs of more northern species have shown a much lower hatching rate when similarly exposed; young hatched from eggs thus exposed to high temperatures are likely to be of lowered vigor. The same principle seems to hold also for northern species that lay eggs so early as to be subject to snow, as actually happens to eggs of Horned Larks, Horned Owls, and other early nesters. The eggs of the Penguins at times are subjected to cold without destroying their hatchability. It is likely that the effect of temperatures between laying and incubation influences both the southern limits of northern species and the northern limits of southern species.

The incubation temperature approaches that of the incubating bird, which ranges from about 100° F. to 110° F. in different species. (It has been reported that the most rapid development occurs at a temperature several degrees above the body temperature for the species.) The normal bird has a temperature rise in the day and a drop at night, but this variation is not so well marked in the incubating bird that remains relatively motionless. (It is said that for the reason of this motionless condition, the incubating, ground-nesting bird gives off little scent.) Actual measurements show wide variations of egg temperature in various parts of the nest. Perhaps the turning of eggs by the incubating bird shifts them about and thereby equalizes development.

The temperature of the egg varies also with construction of the nest. The more substantial and better insulated nests of boreal birds retain heat better than the thinner nests of birds living in a warmer climate. The type of nest construction by a bird may give some indication of the ancestral home of the species. Species invading a warm region from a cold one still construct relatively more solid nests, as their ancestors no doubt did and as their boreal relatives still do. The Corvidae, for example, all build thick nests (Fig. 18·7), even those in the Sonoran Life Zone.

The incubation period of precocial birds lasts longer than that of altricial ones largely because development is carried to a more advanced stage. But when developmental stages are alike, larger eggs tend to require longer incubation periods than do smaller ones. Long incubation periods relative to egg size occur among the Casuariiformes, Apterygiformes, Sphenisciformes, Procellariiformes, Falconiformes, Psittaciformes, Strigiformes, and Trochilidae. Short incubation periods characterize Struthioniformes, Rheiformes, some Anatinae, Turnicidae, Columbidae, Picidae, and most Passeriformes. Knowledge of incubation periods, however, is almost too confused for any conclusions (Nice, 1954).

Development of the Germ Layers. The bird egg is strongly *polylecithal* (which means that it has a large amount of yolk) and *telolecithal* (which means that the yolk is concentrated on one side). The *chalaza* suspends the yolk in the albumen and permits it to rotate so that the embryo rests on the top side (Figs. 6·10, 6·12). Because the bird egg has much yolk, *cleavage* involves only a small disc lying

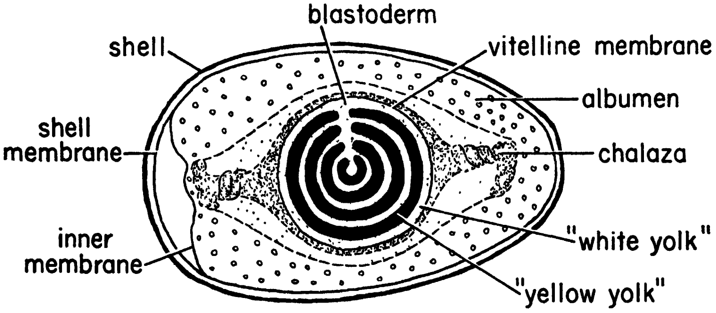


Fig. 6·12. *Diagram of saggital section of a Chicken egg to show structure.*

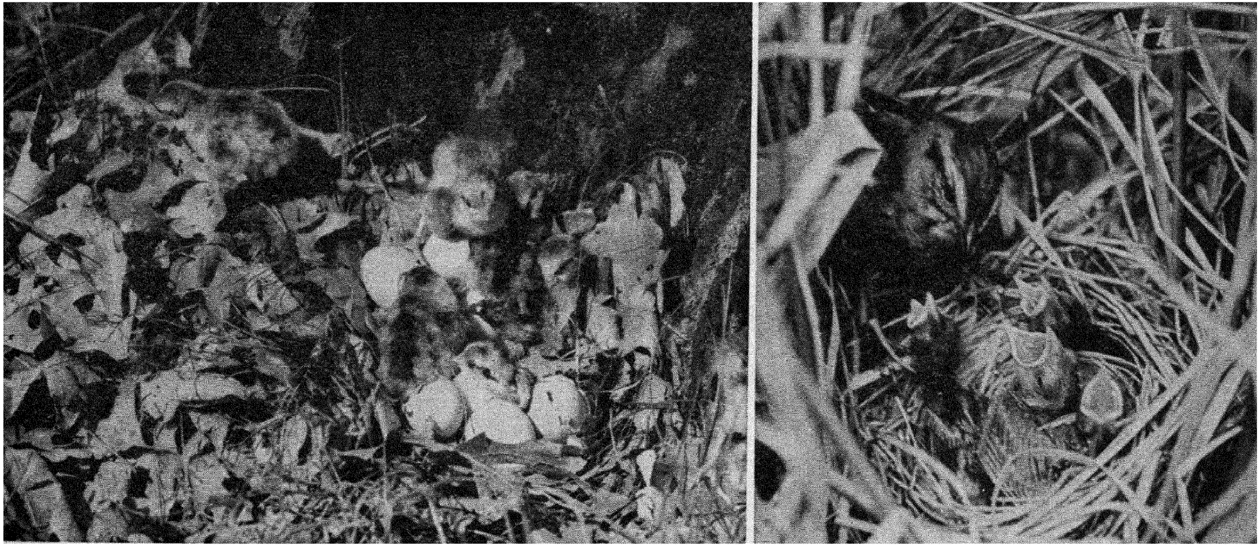


Fig. 6·13. *The Swamp Sparrow (left) feeds its altricial young; the young of the Ruffed Grouse (right) are precocial. (Photographs by F. W. Lahrman, Saskatchewan Provincial Museum, and Wisconsin Conservation Department.)*

atop the yolk. This is sometimes described as *meroblastic discoidal* cleavage. Three layers, *ectoderm*, *endoderm*, and *mesoderm*, give rise to all parts of the body (Fig. 6·11).

Development Rate. After about 27 hours of incubation in the domestic chick, the head begins to take shape at the forward end of the primitive streak and soon the future parts of the brain become distinguishable. By 30 hours the heart is recognizable, and blood vessels soon appear. Blood begins to circulate toward the end of the second day of incubation. Organs for securing food and oxygen and for eliminating waste products follow soon after. These essential acts are carried out by the *yolk sac* and *allantois* (Fig. 6·12). The shell and egg membranes are porous so that carbon dioxide can pass out and oxygen in with considerable freedom. During the fourth day, *limb buds* appear as the forerunner of the future legs and wings. By the fifth day most of the parts of the body have been established. In the Domestic Chicken, the embryo is about half developed by the tenth day and is completely developed by about the twenty-first day.

Although we may speak of birds as *altricial* or *precocial* (Fig. 6·13), depending upon their stage of development at hatching, considerable variation occurs within these groups. It is logical that some intermediate stages between precocial and altricial conditions should occur (page 376). The important matter of comparative embryonic stages of development for different wild species has not received much attention from embryologists.

Birds of higher body temperature have slightly more rapid embryonic development than others. In addition, we may expect that embryos of some species might very well grow faster than those of others. But the large egg of the meat breeds of the Domestic Chicken (3.5 cubic inches) still takes the same 21 days as the ancestral Jungle Fowl with its smaller egg (1.6 cubic inches). The incubation time thus seems to be a fixed part of the hereditary complex of the species.

SUGGESTED READING

PATTON, BRADLEY M., *Early Embryology of the Chick*. Philadelphia: The Blakiston Co., 1952.

PRESTON, T. W., "The Shapes of Birds' Eggs," *Auk*, 70(1953):160–182.

ROMANOFF, ALEXIS L., and ANASTASIA J. ROMANOFF, *The Avian Egg*. New York: John Wiley & Sons, Inc., 1949.

SHUMWAY, WALDO, *Introduction to Vertebrate Embryology*. New York: John Wiley & Sons, Inc., 1948.

*STORER, TRACY I., *General Zoology*. New York: McGraw-Hill Book Co., Inc., 1951.

WEIMAN, H. L., *An Introduction to Vertebrate Embryology*. New York: McGraw-Hill Book Co., Inc., 1949.

WEICHERT, CHARLES K., *Anatomy of the Chordates*. New York: McGraw-Hill Book Co., Inc., 1951.

7

Plumage

It may be redundant to say that unless a creature has feathers, it is not a bird. Yet the possession of feathers does characterize a bird; no other animal has the slightest trace of them. Their origin and evolution belong to that obscurity characteristic both of soft parts and of long-ago. Hardly an adequate theory has been offered for their origin, mute testimony to the remoteness of their beginning and to our consequent lack of knowledge. The theory that the feather originated from a scale in essence suggests that the scale became lengthened and thinned down, its edge frayed out and split, the upper surface to become the feather proper and the lower one the aftershaft. Another theory suggests the mechanism more than the origin. It proposes that the feather developed originally as an outgrowth from the lower layers of the skin and pushed out through the junction between scales.

THE FEATHER

Tracts. Although feathers may grow more or less uniformly over the body of some birds, as in the Penguins, they generally grow in definite places known as *feather tracts.* The term *pteryla* has been applied to a tract and *apteria* to the intervening bare spaces. The terms *ptilosis, pterylosis,* and *pterylography* have been variously applied to feather arrangement. There are eight chief tracts (Figs. 7·1, 7·2).

Head or capital
Spinal or dorsal
Humeral (located on upper arm)
Femoral (located on thigh and running to anus)
Ventral (from chin to anus, dividing along each side of belly)
Caudal (tail feathers and coverts)
Wing or alar (all wing feathers outside the humeral tract)
Leg or crural (all leg feathers except those in the femoral tract)

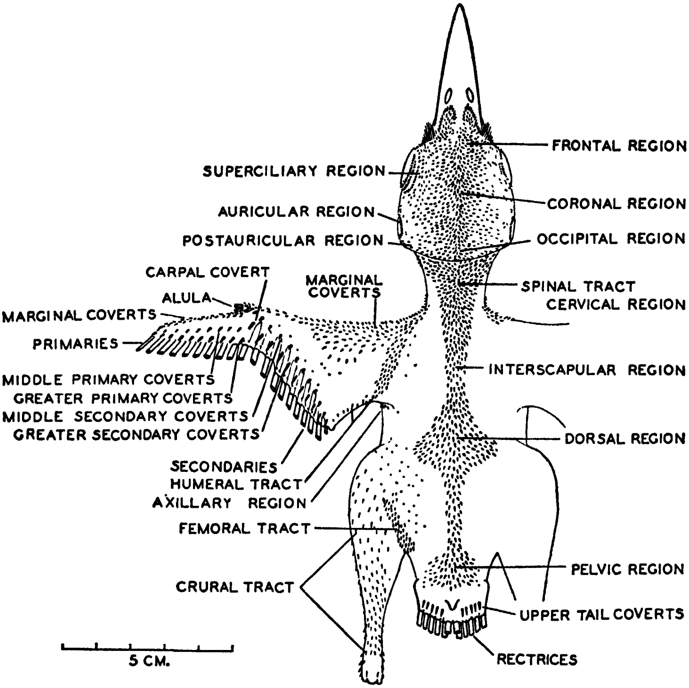


Fig. 7 • 1. *Dorsal view of pterylography of a Passerine bird* (Aphelocoma coerulescens insularis, *Scrub Jay*). (*After Frank A. Pitelka, "Pterylography, Molt, and Age Determination of American Jays of the Genus* Aphelocoma," Condor, *47(1945):229–260.*)

Kinds of Feathers. Four regular types of feathers occur, with an additional fifth kind, the *powder-down feathers* found in some water and land birds. (1) *Contour* feathers, as the name implies, are the outside feathers, the ones that give the bird its shape. (Adult feathers may be called *teleoptiles* to distinguish them from those of the young.) (2) *Down* feathers cover the young bird (in which case they are termed *neossoptiles*); they may also be found in the apterias and tracts of adults (in which case they are termed *plumules*). Scattered through the feather tracts are (3) *semiplumes*, similar to contour feathers but without the interlocking construction of the latter. At the base of the contour feathers are hairlike feathers called (4) *filoplumes* (Chandler, 1916).

Special feathers called *powder-down* have an extraordinary function, at least in the Bittern. They are a most effective "dry shampoo"

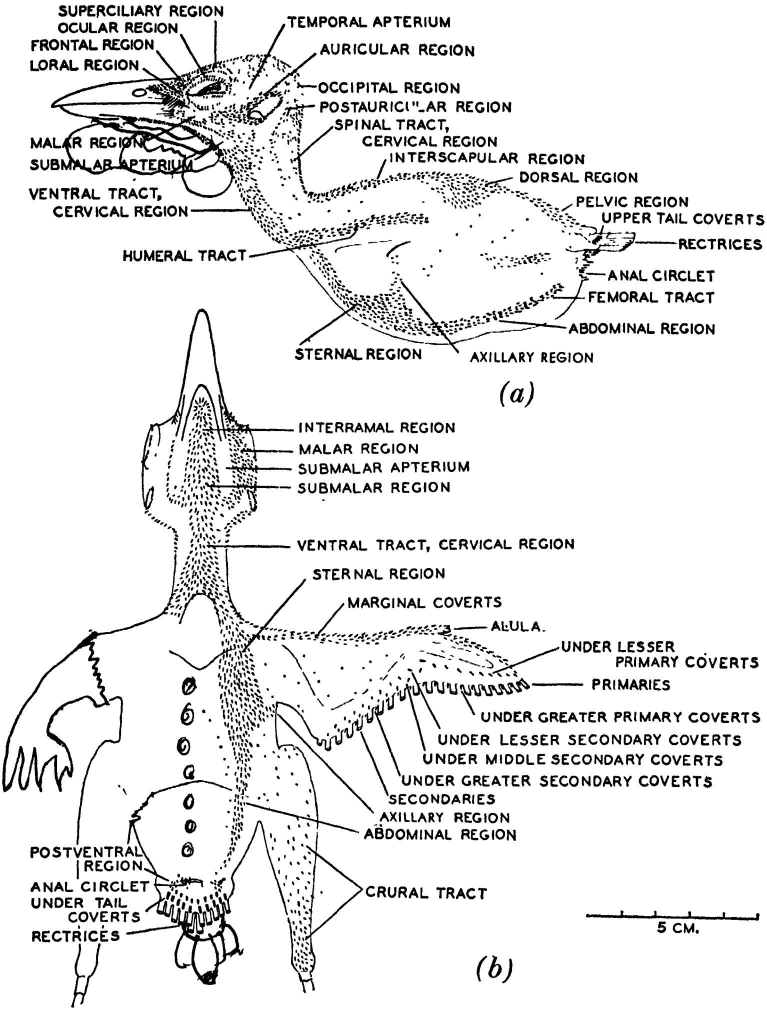


Fig. 7·2. *Lateral view (a) and ventral view (b) of the pterylography of a Passerine bird. (After Frank A. Pitelka, "Pterylography, Molt, and Age Determination of American Jays of the Genus* Aphelocoma," Condor, *47(1945):229–260.)*

for cleaning the plumage, even of such soil as eel slime (Percy, 1951). Other birds have powder-down (e.g., Herons, some Hawks, Wood Swallows). Many birds, especially water birds, use secretions from the oil gland (uropygial gland) for dressing the feathers. Without these secretions, feathers of Waterfowl lose their wet-proof quality and become bedraggled sooner than usual.

Feather Growth. The feather grows from a feather follicle, recognizable in the Chicken embryo at the 144-hour stage when a papilla projects from the skin. The bird skin itself is thin (Fig. 7·3). The dermal layer of the projecting papilla becomes cornified to form the feather, while the mesoderm supplies nutrients only (Fig. 7·4). The feather succeeding the natal down and all subsequent feathers grow by periodic stimulation from the same follicle. The natal down itself is pushed out on the tip of suceeding feathers. But all subsequent feathers grow only after the predecessor departs, which may be by a regular molt or by the irregular loss of the feather. The loss of a feather outside the molting season is enough to stimulate the follicle to replace that feather, but the replaced feather will represent the plumage of the succeeding molt.

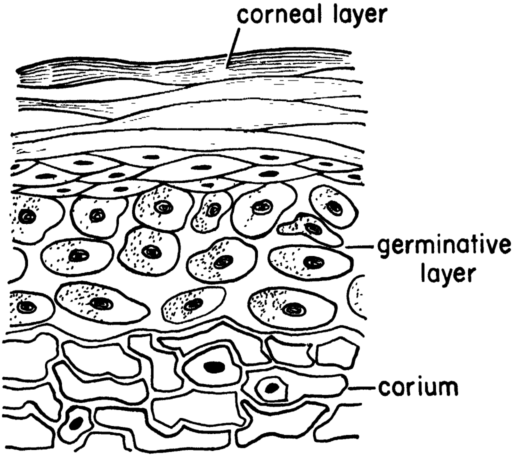


Fig. 7·3. *The bird skin. The integument is characterized by thin epidermis and dermis covering a thicker subcutaneous layer where fat may be stored.*

The cross-barring and growth marks on some feathers indicate daily growth believed associated with drop in blood pressure and increases of mitotic activity at night when the bird is at rest.

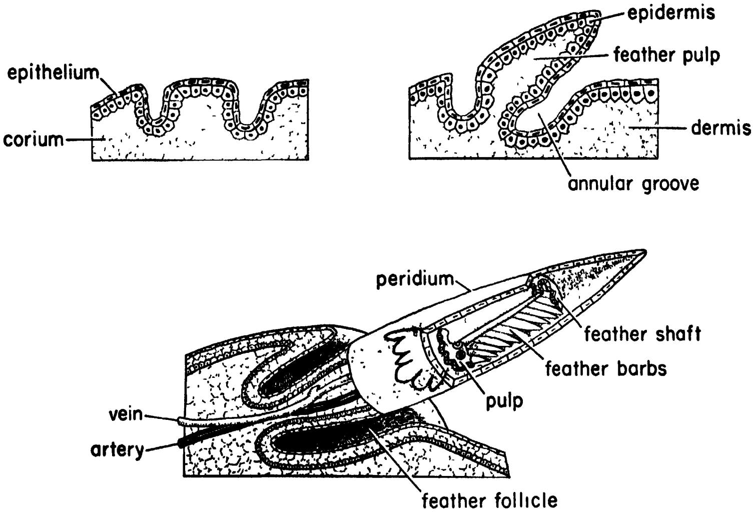


Fig. 7·4. *Development of a contour feather.* (*Top*) *Early stages as seen in cross-section;* (*bottom*) *view of later stage.*

Structure. The feather is indeed a marvel of nature (Fig. 7·5). The *quill* or *calamus* is the part attached to the bird. It is really the body end of the *shaft*; the other end, to which the *vane* or *web* is

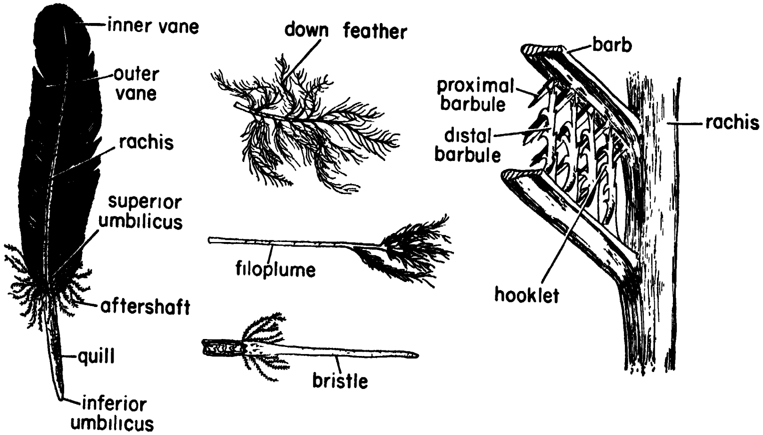


Fig. 7·5. (*Left*) *A contour feather to show the main parts. The inner and outer vanes together form the web.* (*Middle*) *Three types of feathers.* (*Right*) *Two adjacent barbs magnified to show the barbules and booklets that interlock to form a flexible but tight webbing.*

attached, being the *rachis*. The web of the feather consists of processes known as *barbs*, each one bearing further branches called *barbules*, which in turn bear smaller branches called *barbicels*. These barbicels are *hooklets* (*hamuli*) that interlock with adjoining ones to give the feather its webbed effect (Chandler, 1916). The hooklets are so constructed that if they become separated, a little manipulating by the bird's head or bill will put them back together. *Preening* of the feathers is in part restoring of the hooked condition. The number of barbs on a feather may run into the hundreds, barbules into the thousands, and hooklets into the millions.

Under-feathers used for insulation have a fluffier character owing largely to the absence of the hooklets which hold the barbs together. The wing feathers of the flightless Ostrich have no hooklets, which gives them a fluffy, curly character prized by fashion designers. Egret plumes likewise have no hooklets.

Attached near the base of the quill on the inner side of body feathers appears in some birds a small feather called the *aftershaft*. In some this may be only a thread, in others a diminutive feather, and in a very few others (e.g., Emu and Cassowary) it may be as large as the feather itself.

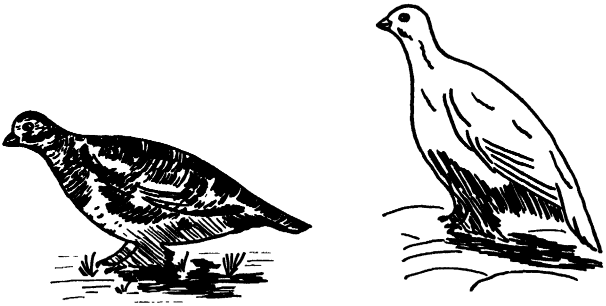
Number of Feathers. The number of feathers on the body varies with the species and possibly with the season. The number seems to vary also with the systematic position of the species. The greatest numbers are present immediately after molt and decline as feathers are lost. In general, larger birds have greater numbers of feathers and water birds have more than land birds. A few actual counts are listed in Table 7·1. (The first four are from Wetmore, 1936.)

Table 7·1
Actual Counts of Bird Feathers

Species	Feather number	Body weight (grams)	Feather weight (grams)
Mourning Dove	2,635	152.7	11.7
American Robin	2,973	–	–
Ruby-throated Hummingbird	940	2.8	.2
Cowbird (female)	1,622	41.4	1.9
Bobolink	3,235	–	–
Cowbird (male)	4,297	(1,246 on head, 3,051 on body)	
Glaucous Gull	6,544	–	–
Domestic Chicken	8,325	–	–
Mallard Duck	11,903	–	–
Whistling Swan	25,216	(20,177 on head and neck, 5,039 on body)	

MOLTS

Number and Sequence. The molt of birds follows well-developed patterns in the various species; some molt once, some twice, and some even three times a year. Molt usually occurs in fall and spring, especially among migratory birds; it may be influenced by day length (Lesher and Kendeigh, 1941). The fall molt thus follows the wear and tear of the breeding season and starts the bird off for migration and winter in a new suit of clothes. In the same way, a spring molt starts the bird out in a new suit for the coming breeding season. The Ptarmigan with its three molts a year changes from the white winter plumage to the brown and white breeding plumage late in winter; during nesting it molts to a gray summer plumage; and in the fall, it goes again to the winter white (Fig. 7·6). (There is one race of Ptarmigan, the Scotch Grouse, which does not don the white plumage.)


SUMMER

WINTER

Fig. 7·6. *The Ptarmigan* (Lagopus) *wears a mottled grayish or brownish plumage in summer but molts to a white one for winter.*

Molts usually begin at one side of an area (as in the primaries) on both sides of the body. In the molt of the primaries, for example, the respectively positioned feathers on both wings drop more or less together (which maintains flight balance), but the sequence may vary somewhat (Fig. 7·7). Gallinaceous birds start the wing molt at the bend and shed the primaries outward. Ducks and Geese, on the other hand, shed all primaries at once, so that for a few days or at most a few weeks, the birds are flightless. In the case of young birds, the sequence of acquiring feathers and the progress of molt can be used as an indicator of age and hatching date. The sequence of tail molt may be

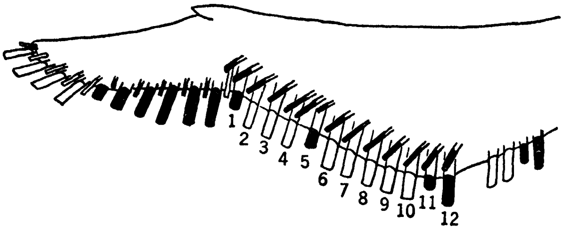


Fig. 7·7. *Dorsal surface of left wing of the Sharp-shinned Hawk to show molt of remiges and greater coverts. Secondaries are numbered. Shaded quills represent new feathers, white quills and feathers, and short quills those that are growing. (After Alden H. Miller, "The Significance of Molt Centers Among the Secondary Remiges in the Falconiformes,"* Condor, *43(1941):113-115.)*

constant or somewhat variable (Fig. 7·8). The rate of growth may become less as the feather grows longer (Figs. 7·9, 7·10). For the Cardinal, however, growth of tail feathers has been recorded as 0.08 inches for sixteen days, 0.11 for the next seven days, and 0.12 for the next four. The average daily growth for the Carolina Chickadee has been reported as 0.05 inches and for the Red-eyed Towhee, 0.08.

Altricial birds generally hatch in a near-naked condition (Fig. 6·13), about the only feathers being a few tufts on the head and in the feather tracts (page 376). Most or all Woodpecker young are naked.) In precocial birds like the Domestic Chicken the body is clothed in *natal down.* The molt by which down is replaced by the *juvenile* (sometimes called *juvenal*) *plumage* is termed postnatal molt.

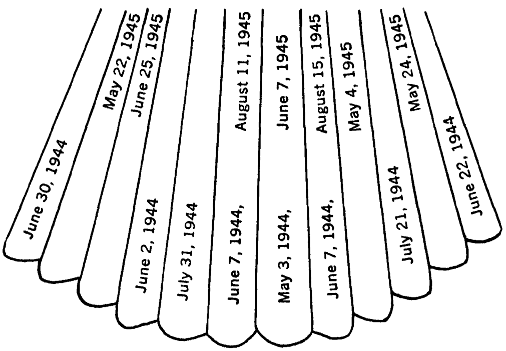


Fig. 7·8. *Replacement dates of tail feathers in a young female Golden Eagle (hatched April 19, 1943). (After Malcolm Jollie, "Plumage Changes in the Golden Eagle,"* Auk, *64(1947):549-576.)*

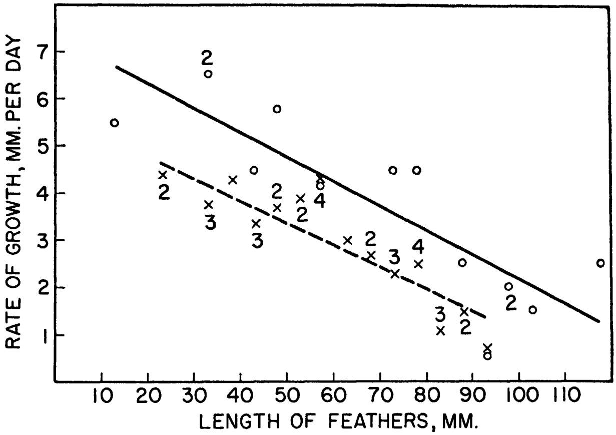


Fig. 7·9. *The feather grows more slowly as it lengthens (Red-shafted Flicker). Circles and solid line are primary feathers, crosses and dashed line are secondaries. The numerals indicate number of data for each calculation. (After Frederick H. Test, "Molt in Flight Feathers,"* Condor, *47(1945):63–72.)*

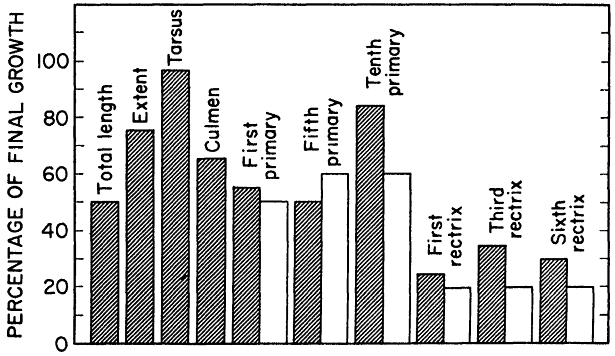


Fig. 7·10. *The percentage of final growth attained by nestling Long-billed Marsh Wren (shaded bars) and House Wren (unshaded bars) by the twelfth day of growth. (After Wilfred A. Welter, "Feather Arrangement, Development, and Molt of the Long-billed Marsh Wren,"* Wilson Bulletin, *48(1936):256–269.)*

The juvenile plumage in altricial birds develops in the nest so that they are well attired before departing. Precocial birds depart from the nest when they still have natal down. The juvenile plumage is lost at the *postjuvenile* (sometimes called *postjuvenal*) molt, by which the first winter plumage is obtained. This plumage may differ from that of the adult or it may be similar. The first winter plumage remains all winter, after which the *prebreeding* (*prenuptial*) *molt* of late winter or early spring changes the plumage from the first winter to the *breeding* (*nuptial*) *plumage.* In some species, the young birds during their first breeding season retain an immature type of plumage, which is designated as the *first breeding* plumage to distinguish it from the fully adult type. This may occur in males of the American Redstart and Red Crossbill.

The breeding plumage is shed during the *postbreeding* (*postnuptial*) molt. In cases where the birds require several years to attain the full breeding plumage, this would be called *first postbreeding* molt. The plumage donned is called the *winter plumage.* It usually is the same as the plumage worn the previous winter by birds of the previous year's age class. If it differs from that of the first winter, it would be termed the *second winter plumage.* This plumage is lost at the second prebreeding molt. Only in a few cases (a few Eagles, Gulls, and others) does the difference in plumage continue. If it does, the plumages would be called second, third, or fourth breeding plumages, and third or fourth winter plumages; the molts would have parallel names.

Eclipse Plumage. Among a few ducks (perhaps more than is generally realized), the male changes at the postbreeding molt into a plumage resembling that of the female. In a short time, usually only a few weeks, the bird molts again into the characteristic male plumage. This transitory summer plumage is called the *eclipse plumage.* Its appearance has long been known for the spectacularly colored Mallard and Wood Ducks. The eclipse plumage is said to represent the winter plumage worn for a short time and then to be lost by a shift of the prebreeding molt from the end of the succeeding winter forward several months to appear in summer. The plumage worn most of the year may really be the breeding plumage (Pettingill, 1956).

Moltless Change. Though changes in plumage ordinarily occur at molts only, a few birds have special means by which a plumage color or pattern change occurs without molt (though the feathers themselves change only at molt) which is termed *aptosochromatism* (sometimes *aptosochroism*). Several birds acquire the breeding plumage by wear or breaking of feather tips. The male of the common House Sparrow wears a long black "bib" in the breeding season. But in the winter season, this black area is much restricted because of gray feather tips which hide it. These wear or break off during the late winter and the full black front appears by the breeding season

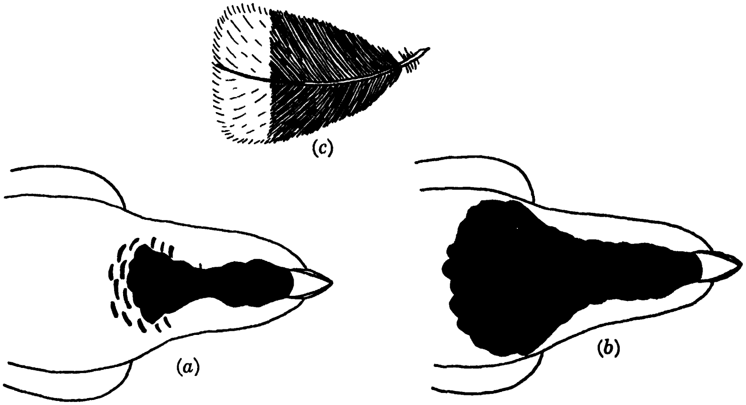


Fig. 7·11. *The change in black from the narrow "bib" of winter* (*a*) *in the House Sparrow to the breeding plumage* (*b*) *takes place by the breaking off of the gray tips* (*c*) *to reveal the black underneath.*

(Fig. 7·11). In the same way, the male Bobolink dons his handsome black and white breeding plumage by loss of yellowish tips hiding the black. A brownish wash over the wintering Snow Bunting hides the fact that the feathers themselves are largely white. In spring the brown tips fall away to reveal the clear white of the breeding plumage.

In all cases, however, one must bear in mind that any color is likely to fade. The clear browns, reds, or blues may fade greatly as the season progresses, so that they may have changed their appearance markedly by the time of molt. The green of the Cissa or Chinese Jay changes to blue in museums and zoos owing to the evaporation of volatile yellows. The deep orange-yellow plumes of the Twelve-wired Bird-of-paradise fade to pale lemon-yellow in museums. In addition, soiling and mechanical wear may materially alter the plumage.

COLOR

The Nature of Color. Feathers achieve color in two standard ways, one chemical and the other structural, but our knowledge of the subject leaves much to be desired. Some colors appear to involve both chemical pigments and the structural break-up of light.

Animal pigments are sometimes called *biochromes*, of which three are reported to be common in birds: *carotenoids*, *tetrapyrroles*, and *melanins*. The carotenoids are red, yellow, and orange pigments of a fatty nature. They give red color to feathers, for example, as well as the yellow in the legs and bills of some birds. Some yellow feathers may carry a carotenoid pigment, while others may be yellow from structural color.

Tetrapyrroles may be of hemoglobin pigment (*porphyrins*) or bile pigments. The former gives the red color to the comb and wattles of the Domestic Chicken. The bile pigments may give eggshells either the ground color or markings. Two tetrapyrrolic pigments may well be mentioned because of their unique character: *turacin*, a red pigment (containing copper); and *turacoverdin*, a green pigment. Both are found in species of Musophagidae of Africa.

Melanins are usually brown, and in concentration they appear black, as in the Raven. Both the physical and the chemical nature of the melanin may vary the color.

Structural colors are reported as solid colors or as iridescent ones. The neck feathers of Grackles show black, but when the light strikes at the right angle from the observer, they appear as a metallic green or purple. The throat of the Hummingbird likewise shows iridescence in a pronounced manner.

Small irregular cells overlying pigment granules (melanin) break up the light falling upon them; the broken-up light thus shows against the dark background of the pigment (Fig. 7·12). Such structural colors can be altered physically, but not by chemicals unless the

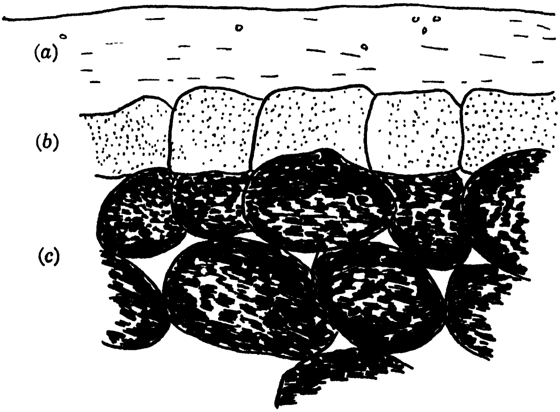


Fig. 7·12. *The color-producing cells in the Blue Jay feather. (a) Cornified layer, (b) color-producing layer, and (c) layer of pigment granules. (After Carl Gower, "The Cause of Blue Color as Found in the Bluebird* (Sialia sialis) *and Blue Jay* (Cyanocitta cristata)," Auk, *53 (1936):178–183.)*

reflecting cells are penetrated and filled by a chemical or the underlying pigment is bleached. If the structure is altered physically as by crushing or grinding, the color disappears. Pigment colors, on the other hand, can be ground or crushed without changing their color.

Abnormal Colors. Variations of normal color appear in the wild and others can be induced in the caged bird. Stains and soil are sometimes called *adventitious* colors. The rusty color sometimes seen on the plumage of Swans and Snow Geese is of this nature. Woodpeckers develop a very dark breast from rubbing against tree trunks, and Crossbills may also get very dark from pitch and other soil. House Sparrows living in cities acquire a dark soil of soot which their country cousins do not. American Sparrow Falcons that feed upon grasshoppers in burnt stubble will get very dark.

An absence of pigment results in white, and the condition is called *albinism.* All light rays are reflected by the "pigment holes" thus left in the feathers just as foam on a wavy sea looks white from the same type of reflection. The defect resulting in albinism may be complete (in which case the bird has pink eyes and soft parts) or partial, and involve only a patch of feathers or even a single one, which will show white in place of normal coloration. Temporary albinism may be caused by dietary or circulatory deficiencies at the time of feather formation.

Albinism is distinct from white coloration, as in the entire plumage of Swans or in the few spots on a Robin's body. Such white coloration does not involve the soft parts, and the eyes, legs, and bill have the usual color. Genetic studies show that among breeds of the Domestic Chicken, some white patterns (even the entire plumage as in White Leghorns) are *dominant* over color, the genes for the latter being recessive (Chapter 20). Albinism when inherited is recessive to the normal plumage. White plumage grown by the adult and young Ptarmigan at the postbreeding and postjuvenile molts, respectively, is a true white one, not albinism. (It may be added that the white plumage will come and go at the proper seasons, snow or no snow.) Albinism has been reported in America for many birds, among them the American Crow, Raven, Bronzed Grackle, Cowbird, Red-winged Blackbird, House Sparrow, American Robin, Chimney Swift, and Barn Swallow. Albinos may be accepted with little discrimination among some species at some times, or they may be harrassed by other members of the species.

Albinism has been classified as *total albinism*, *incomplete albinism*, *imperfect albinism* (*dilution*), and *partial albinism.* The last named may be *random* or *specific* (Nero, 1954).

In addition to albinism, abnormal color conditions have been found and named *melanism*, *erythroism*, and *xanthochroism*. Melanism occurs by an excess of brown or black in the feathers. It has been reported in the Snipe and Skylark, and it occurs fairly often among some Hawks, notably the American Rough-legged Hawk and the Swainson Hawk. It seems established that these two species have melanism as a color phase.

Erythroism, the excess of red, occurs rather uncommonly in nature. In the 1920's, it appeared in Bob-whites of the southeastern states, but practically disappeared in a few years (page 395). Breeding experiments showed that it was inherited as an apparently incomplete dominant character. Both wild and confined birds exhibited a weaker condition than normally colored ones (Cole, Stoddard, and Komarek, 1949). Most mutations seem to accompany physical weakness; red *color phases*, however, are normal in some birds and the birds do not exhibit physical weakness.

Xanthochroism appears in Parrots, with yellow pigment replacing the green. In the West, Red-shafted Flickers appear with orange, yellowish-orange, or even yellow where the color should be red, or orange-red. The Pacific Northwest reports more such birds than areas nearer the Yellow-shafted Flicker range. This is in accord with the belief that such birds are not hybrids (page 391) but possible cases of xanthochroism, probably through absence of the normal red.

Dimorphism. *Color phases* of normal dimorphic conditions are termed *dichromatism*. The Screech Owl, for example, appears in red and gray color phases. Highway kills in Wisconsin showed 61.3 per cent to be the gray phase. Red and gray color phases also occur in the Pygmy Owl and Ruffed Grouse. Such color phases may be distributed regionally, so that in some areas one phase is common and in others it may be rare. There is evidence to indicate that the Blue Goose is a regional color phase of the Snow Goose. If males and

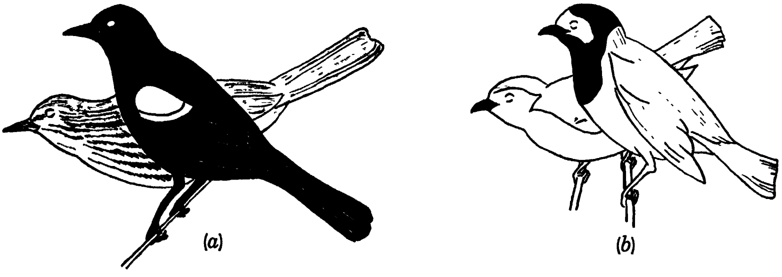


Fig. 7·13. *The Red-winged Blackbird (a) and Hooded Warbler (b) illustrate sexual dichromatism. The front bird of each pair is the male.*

females differ in shape or color, it may be termed *sexual dimorphism* or *dichromatism*, respectively (Fig. 7·13). Often this involves appreciable difference in size.

USE OF COLOR

Coloration in the bird world has both visual and nonvisual values. The nonvisual ones themselves perform general functions irrespective of species, whereas a particular visual use may be the property of a single species only. No doubt color itself functions in both pattern and posture, as seen in courtship activities (Chapter 18).

The three nonvisual values are absorption of light or heat rays, reflection of these waves, and the deposition of excretory products. It is well known that dark objects absorb more light and heat rays than lighter colored ones. Possibly the lighter plumages of desert birds serve in part for reflection of light and heat rays, along with the protection to the bird offered by protective coloration. A bird absorbs radiation directly from the sun, reflected from sky and clouds, and reflected from earth and objects. It will radiate long infrared rays (Fig. 7·14).

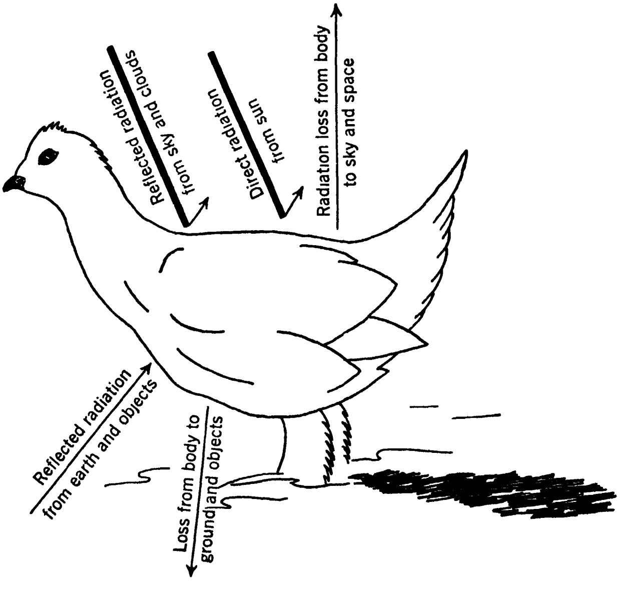

Reflected radiation from sky and clouds
Direct radiation from sun
Radiation loss from body to sky and space
Reflected radiation from earth and objects
Loss from body to ground and objects

Fig. 7·14. *A bird receives heat by radiation from the sun directly, reflected from sky particles and clouds, and reflected from the earth and objects. It will lose long infrared rays by radiation.*

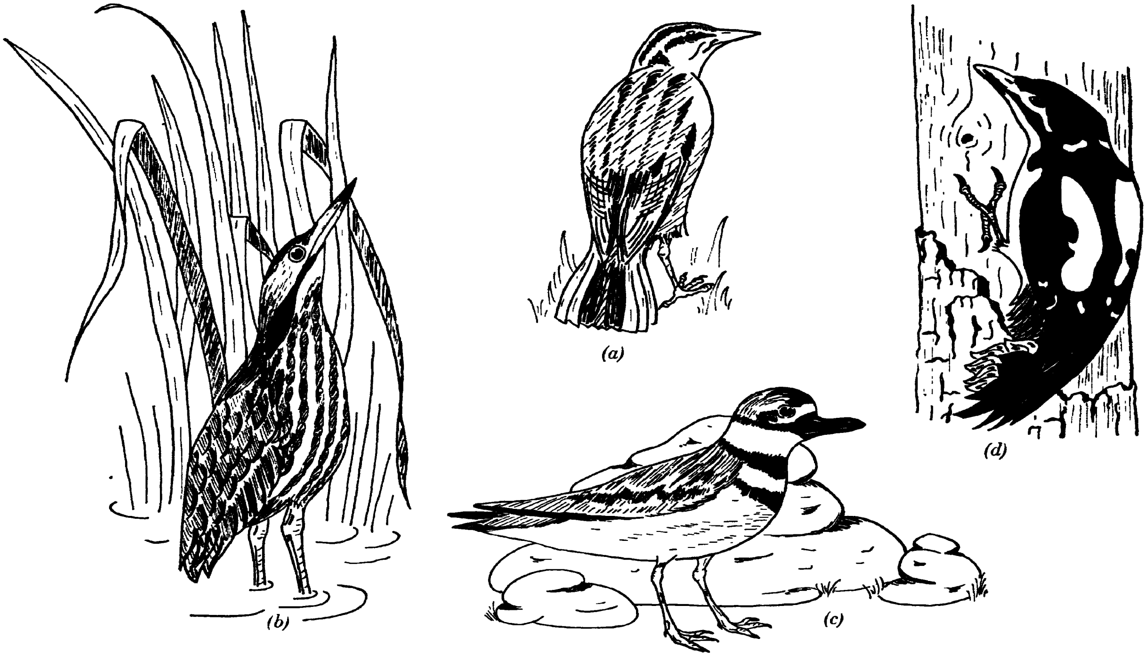


Fig. 7·15. *Colors and patterns may be used alone or in combination with posture and placement. The Bittern (a) remains motionless in the vegetation and thereby goes unnoticed. The pattern and color of the Meadowlark (b) helps conceal the bird, but it flicks the white outer tail feathers, perhaps to warn others. The Kildeer at (c) has a ruptive pattern that helps it to blend into its background. The Woodpecker at (d) is displaying its tail patch to intimidate another.*

The many visual values of coloration require careful and judicious study, which in the light of our present knowledge can hardly be at all complete. No doubt many colors and patterns have more than one value, which is somewhat the same as saying that they have more than one function. Colors as we see them may not be the same as those seen by the bird, just as the eye and photographic film do not "see" color the same way. They may not even be seen the same by the bird's enemies, friends, or prey.

Visual values may be conveniently listed as *concealing* colors, *warning* colors, *recognition* colors, and *display* colors. All are associted with pattern, posture, position, and placement (Fig. 7·15, 7·16).

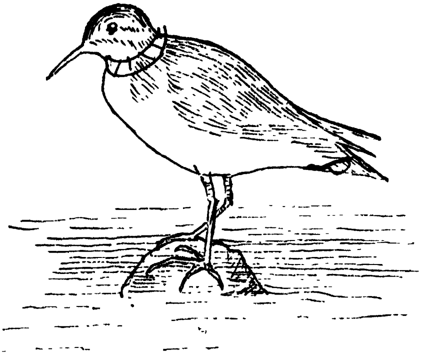


Fig. 7 · 16. *The lighter under parts break up the solidity of the body by obliterating the usual shadow.*

Concealing Coloration. Concealing coloration serves to protect its posssessor from detection by its enemies or prey as the case may be (page 153). The grayer colors of the desert birds may help them to blend into the gray desert vegetation. The general brownish streakings of so many grass birds may conceal them in the vegetation. The Bittern is well known for its combining color and pattern with posture to effect concealment (Fig. 7·15). It will stand still with neck and head extended vertically. It even will turn its neck and head slowly as an observer moves about, always presenting the well-blending front. If need be, it will sway with the wind-blown vegetation, presumably to further the deception.

Grouse nest on the ground, and the females particularly blend with the ground for concealment. The Ruffed Grouse wears browns to match the humid forest floor, as do also the females of the Spruce and Franklin Grouse. The female Blue Grouse of the interior is gray in accord with the grayer aspect of the dry landscape. This is in contrast to the browner female Blue Grouse of the more humid coast. The Bob-white, Meadowlark, Snipe, Nighthawk, and others show similar concealing patterns.

But some of the Plovers and other birds of the shore zone wear rather bold *ruptive* patterns (disruptive) that break up the body outline and effectively camouflage it. This tendency for bold ruptive patterns seems an effective technique for many birds of the shore. It is used rather freely also by birds of the treetops and of many other habitats.

Many birds are difficult to see, even in the open, because of *counter shading*. The Shorebirds have light under parts, which break up the solidity of the body by lightening the part the eye of an observer expects to appear dark from a shadow. The dark back also breaks up the solidity normally given by highlights, so that the bird "flattens" into the background (Fig. 7·16).

Flash Colors. Many birds have brightly colored patches that may serve to give warning, as when a Mockingbird flashes its white wings as it approaches an interloper. When startled, the Meadowlark flashes its white tail. It does so also in conflict with other Meadowlarks. In some cases, the sudden flash of white or other color may confuse a pursuing enemy, as when a Meadowlark suddenly flashes its white tail in a Cooper Hawk's face before dropping into the grass. A Meadowlark upon alighting may flash the white tail patches and then quickly creep off a few feet, which act has been interpreted as an action (common to many birds) to cause a "positional confusion" by attracting attention to the place where the bird no longer can be found. Inasmuch as birds of prey seldom continue a chase once foiled, this may be an effective trait.

Recognition Marks. Mammals use their sense of smell to determine the species and sex of another animal and also to ascertain whether it is friend or foe. Compared to gaily colored birds, no mammal has brightly colored fur, and few even have bright markings or striking patterns. It seems logical that bird colors in part have evolved so that one bird may recognize another or be recognized itself. Among birds of striking colors, there appear to be innate recognition patterns; among somber-colored species, these patterns seem to be associated with posture and display. The Cardinal seems to have no trouble in recognizing a male as such, but the male Mockingbird apparently must bristle up to every new Mockingbird before finding out whether it in turn bristles up like a male or acts submissive like a female. But a Mockingbird seems quite able to recognize its mate after they have paired, and this ability seems to be associated with shape, action, carriage, voice, and many other individual attributes of an animal (see also Chapter 18).

Among Yellow-shafted Flickers, the male bird wears marks under each chin, like mustaches (Fig. 7·17). An experimenter added an artificial mustache to the female of a pair and her mate promptly attacked her as he would an intruding male (Noble, 1936). Cock feathers affixed to the tail of a hen will get the same response from roosters. It seems certain that these male marks are recognized by others as denoting a male.

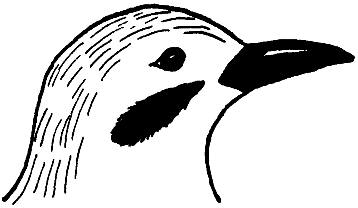


Fig. 7·17. *The "mustache" on a Flicker signals maleness to other Flickers.*

The white in the tail feathers of a Junco probably serves as a recognition sign to keep the flock together in winter. Anyone who has watched a flock can detect the flash of white in the tail as a bird flies. The twittering of a flock no doubt is also part of the recognition and flock-maintenance mechanism.

Display Coloration. The large number of known examples of coloration associated with display leaves little room for doubt as to their purpose, although observers may conscientiously differ in interpreting bird behavior (Fig. 7·18). Birds having conspicuous patches of color are prone to exhibit them in characteristic ways and at definite times, all of which suggest a purpose, but we must not confuse this with consciousness (see Chapter 18). Many of the color patches used in display no doubt serve as signaling devices (*semantic colors*). The American Redstart's brilliant patches of red amidst the black on body and tail probably serve variously as ruptive patterns, recognition marks, and display patterns. Anyone who has watched the Redstart fan out its tail will appreciate the apparent emphasis by this bird on display of the color and pattern in its plumage.

The male Ruff of Europe has a large resplendent collar which he may suddenly open immediately in front of the female. Many Woodpeckers have display colors which they show, such as the red or yellow linings of tail and wings of Flickers, displayed in courtship and conflict. The Greater Spotted Woodpecker displays the red under-tail before a rival much as a Flicker does (Fig. 7·15). The Killdeer, along with many other birds, feigns injury to attract an intruder from its nest or young. Prominent in the Killdeer act is the display of the rusty red upper tail coverts (Fig. 7·18).

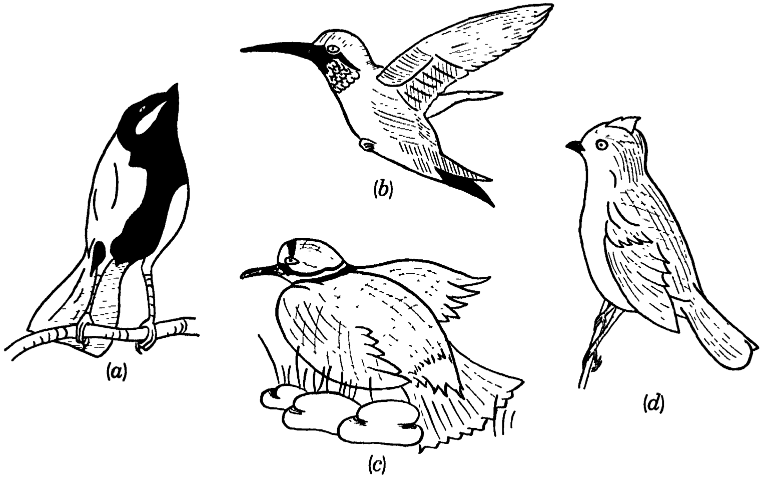


Fig. 7·18. *Display of breast, throat, tail coverts, and crest by (a) Tit, (b) Hummingbird, (c) Killdeer, and (d) Kinglet.*

The display performances of the Tetraonidae have long been known, but many other gallinaceous birds also carry on elaborate displays. Among the commonly known ones are those of the Turkey and Peacock. In the case of the Turkey, the bare skin of the head may become surcharged with blood and change from a steel blue to a bright red. The combs over the eyes of the displaying male Blue Grouse (commonly called "Hooter" by westerners) change in display from a yellow to a brilliant orange-red.

SUGGESTED READING

*ALLEN, ARTHUR A., *The Book of Bird Life.* New York: D. Van Nostrand Co., Inc., 1930.

*ALLEN, GLOVER M., *Birds and Their Attributes.* Boston: Marshall Jones Co., 1925.

*ARMSTRONG, EDWARD A., *Bird Display and Behavior.* London: Lindsay Drummond, Ltd., 1947.

*ARMSTRONG, EDWARD A., *Bird Life.* New York: Oxford University Press, 1950.

BOULTON, RUDYARD, "Ptilosis of the House Wren (*Troglodytes aedon aedon*)," *Auk,* 44(1927):387-414.

CHANDLER, ASA C., *A Study of the Structure of Feathers, with Reference to Their Taxonomic Value.* University of California, Publications in Zoology, 13(1916): 243-446.

COTT, HUGH B., *Adaptive Coloration in Animals.* New York: Oxford University Press, 1940.

DWIGHT, JONATHAN, JR., "Sequence of Plumages and Molts of the Passerine Birds of New York," *Annals of the New York Academy of Science,* 13(1900):73-360.

LILLIE, FRANK R., "The Physiology of Feather Pattern," *Wilson Bulletin,* 44(1932): 193-211.

MAYER, F., and A. H. COOK, *The Chemistry of Natural Coloring Matters.* New York: Reinhold Publishing Corp., 1943.

MICHENER, HAROLD, and JOSEPHINE R. MICHENER, "The Molt of House Finches of the Pasadena Region, California," *Condor,* 42(1940):140-153.

SUTTON, GEORGE MIKSCH, *The Juvenal Plumage and Post-Juvenal Molt in Several Species of Michigan Sparrows.* Cranbrook Institute of Science, Bulletin No. 3, 1935.

THAYER, GERALD H., *Concealing Coloration in the Animal Kingdom.* New York: The Macmillan Co., 1909.

8

Age and Sex in the Bird

Our knowledge of age and sex ratios in wild birds is scanty at best, and this chapter assembles some available information on these important subjects. Further material will be included in other chapters, such as those on bird ecology. Because the sex of a bird can often be told at a glance, our knowledge of sex ratios and their distribution may be more extensive than our knowledge of age.

The following terms have been suggested (Wood, 1946) to designate young birds: *nestling*—not ready to leave the nest; *fledgling*—ready to leave the nest but still under parental care; *juvenile*—out of the nest but its postjuvenile molt not yet completed; *immature*—in its first winter plumage.

AGE FACTORS

There are five factors that must be considered in discussing age. The first is *life expectancy*, which means the time left to the individual at any particular age. Life expectancy differs from the *average age*, which is the average for the population or group as a whole. The *maximum age* is still a third factor, and probably represents the potential years that an organism might survive before biological breakdown puts an end to it; no doubt the maximum age in this sense is seldom reached. By the *age of maturity* is meant the age of sexual maturity, for an animal should be considered as mature only when it is capable of reproducing itself. It varies among species, but most common birds reach sexual maturity in their first year of life. There appears to be considerable "biological latitude" in age of sexual maturity. The Jungle Fowl breeds at 1 year of age, but some Domestic Chickens will lay fertile eggs at 6 months and sometimes even at 4 months of age. The *maximum breeding age* has little practical significance in nature, for it is evident that few birds are successful enough in coping with the vicissitudes of life in the wild to outlast the capacity for reproductive life.

Life Expectancy. As yet we have few data on the life expectancy of wild birds. The mortality of young birds may reach as high as 75 per cent during the first year and continue henceforward at the rate of 45 per cent per year. But it varies among species and perhaps geographically as well and may reach 60 per cent in some and be lower in others. The life expectancy of the American Robin when fledged seems to be about 14 months. The life expectancy of the Herring Gull when fledged, on the other hand, seems to be about 30 months. The average fledged Grouse or Quail has a life expectancy of about 1½ years. A study of the Ovenbird (Hann, 1937) shows that the female may have a life expectancy of about 29 months and the male of about 34 months. (Yet there are indications that the female among birds tends to outlive the male, just as in man.)

Longevity. The term *longevity* has several shades of meaning for various writers, but basically it means the *duration* of natural life. A popular rule of thumb gives the age an animal should attain as six times the number of years needed to reach maturity. We do not know how true any rule of this sort is for mammals, and we know less of its truth in birds. The Raven, which matures at the age of 1 year, for example, may live a decade or more.

Known advanced ages among birds in the wild are few. The Ovenbird has been reported to live 7 years; 7 years has been reported for the Yellow Warbler, Myrtle Warbler, Pine Warbler, and Yellow-throat. It may well be, therefore, that 7 years is the "three-score-and-ten" for Warblers and other small birds.

Banded Cardinals have reached 14, 16, and 21 years, respectively, and banded Mallards have reached the advanced age of 15 years in the wild. Reports of age in wild birds are subject to error unless the birds have been marked for complete identification, but recognizable individual Herring Gulls have lived 24 years, the Black-backed Gull 63.

Records of age among birds in captivity suggest the potential age of birds. A bird that successfully adapts itself to life in captivity conceivably could live out the potential life of the body mechanism. The uncertainties and dangers of life in the wild exceed those of birds in the zoo; yet we must not forget that captive birds live artificial lives.

As we are interested at the moment not in natural life of the caged bird but in the lasting possibilities of the avian body mechanism, we can overlook the artificiality of captivity. Tame Parrots have been reported to attain great age. Definite evidence indicates that an Eagle Owl has lived to 68 years in captivity (Griswold, 1953), which is the all-time bird record. Other reported ages are: Condor, 52 years; Pelican, 40 years; Passenger Pigeon, 29 years; Rose-breasted Grosbeak, 18 years; and the Cardinal, 21 years.

The actual age reached by birds in the wild varies from these examples of long life. The expected longevity for several species has been calculated from returns of banded birds and mortality rates. Table 8·1 gives some examples of mean natural longevity of Passerine birds.

Table 8·1

Mean Natural Longevity of Some Passerine Species

Species	Longevity (Dated from)	Longevity (Years)	How Obtained *
American Robin	First Jan. 1	1.3	B
American Robin	First Jan. 1	1.4	C
European Blackbird	First Jan. 1	1.9	B
Song Thrush	First Jan. 1	1.6	B
British Robin	First Aug. 1	1.1	C
European Redstart	Breeding Season	1.1	C
Song Sparrow	April	2.0	C
Song Sparrow	April	1.9	B
Starling (England)	First Jan. 1	1.6	B
Starling (Netherlands)	First Jan. 1	1.5	C
Starling (Switzerland)	First Jan. 1	1.1	B
Ovenbird	Breeding Season	1.7	C
Great Tit	First Nov. 1	1.4	C
Great Tit	First Nov. 1	1.1	C
Blue Tit	First Nov. 1	1.4	C
Marsh Tit	First Nov. 1	1.6	C
Rook	Nest departure	1.4	B

* B—banded young recovered at death; C—calculated from mortality rate.

Source: Donald S. Farner, "Age Groups and Longevity in the American Robin: Comments, Further Discussion, and Certain Revisions," *Wilson Bulletin,* 61(1949): 68–81.

AGE AND POPULATION

Composition of a Population. Any population of birds at any one time consists of individuals of all ages and of both sexes. The age composition varies with species, but consists of three classes: *young birds, mature individuals,* and a few that may be classed as *aged.* Common dooryard birds reach maturity in a year, and often birds of the year become indistinguishable from adults by fall. Earlier in the season, two general classes, adults and immatures, can be identified; still earlier there may have been adults, immatures, juveniles, and nestlings. Birds that take several years to mature may be distinguishable by year classes, though this seldom happens.

Some idea of age distribution appears possible from banding returns. For Bob-white with a life expectancy of about 18 months, the composition of the breeding population has been variously indicated as, for example, 75 per cent second-year birds, 18 per cent from the second preceding year, and 7 per cent from earlier years. Although losses presumably are heaviest among the weaker birds—the first-year birds and those past their prime—the general proportion of first-year to older birds seems to be about 50 per cent, but it may reach 60 per cent of the total population. No doubt the differences in published reports reflect paucity of study, variations from year to year, variations from region to region, and variations with habitat. The study of age classes in the various seasons is indeed a most fruitful theme of investigation, but one where data are gathered slowly and painstakingly.

In trying to pin down concepts of the number of birds of each age in the population of birds, one must of necessity select some specific date as a base of operations. As life goes on all the time, age data are continuously changing. Various dates have been chosen by various people, some rather abstract like "fall" or "winter," some by calendar time. Data for the English Robin, based on the birds estimated to be alive on August 1 indicate that two-thirds of the birds are young of the year and about a fifth are from the year before; the rest would be of earlier years (Lack, 1943). Using January for the American Robin, the birds of the year form about half and those of the year before about a quarter of the whole population (Farmer, 1949). About

Table 8·2
Age-Class Percentages of Some Species

Species	Year Class								
	1	2	3	4	5	6	7	8	9 and Above
	Per Cent								
Ring-necked Pheasant	71	21	6	1	–	–	–	–	–
Valley Quail	72	20	5	2	1	–	–	–	–
Herring Gull	47	19	12	8	6	3	2	1	2
Mourning Dove	69	17	7	4	2	1	–	–	–
Mockingbird	33	23	13	10	8	8	2	1	2
American Robin	53	25	13	6	2	1	–	–	–
English Robin	67	19	10	3	1	(?)	–	–	–
Song Sparrow	58	28	10	3	1	Trace	–	–	–

two-thirds of the Mourning Doves are birds of the year (Quay, 1951) but only a third of the Mockingbirds (Michener, 1951). The very great difficulties in gathering data make for scarcity of such records and for impossibility of forming many generalizations. Table 8·2 gives data as variously reported for several species. What they indicate other than that young birds outnumber older birds, and the older the birds, the fewer there are, is difficult to say. Some day more can be said. Persistence of Mockingbirds into the 7-, 8-, and 9-year age classes is rather surprising as compared to other small land birds. Because the Herring Gull takes several years to become fully adult, it would be expected that there would be more birds in the older age classes than for a bird maturing in one year.

Seasonal Changes in Age Classes. In addition to the age classes with respect to the population as a whole, a marked seasonal pattern of age classes occurs. The proportion of young in the general population rises markedly during the breeding season when it reaches its peak for the year. It declines progressively, though not necessarily at a constant rate, to about the starting number by the next breeding season. Some variation can occur from year to year; probably it does rather often. A bad nesting season for a species might locally result in almost no production of young birds. Accordingly, the adult-young ratio would be high for the adults and low for the young. Yet in the long run, the over-all ratio should remain relatively fixed for a species (perhaps also for a region).

Counts of the number of young and adults are rather more easily obtained than those measuring the actual age of the birds. The several techniques for identifying young birds (that is, birds of the year)

Table 8·3

Adult-Young Ratios Reported from the Field

Species	Number of Young per 100 Adults	Date
English Robin	197	August 1
Herring Gull	107	August 1
Song Thrush	107	August 1
Starling	101	August 1
European Blackbird	93	August 1
Lapwing	54	August 1
Mourning Dove	154	September
Mourning Dove	117	September
Herring Gull	89	September 1
Valley Quail	235	November
Bob-white	331	November-December
American Robin	192	January 1
American Robin	113	January 1

have resulted in a number of records of adult-young ratios. That they may differ among themselves or with data such as those given in Table 8·2 is only to be expected. Differences in reports may arise from differences among species, local differences in bird life, differences in breeding seasons, differences in sampling methods, differences in time of counts, and sometimes plain mistakes. Table 8·3 gives examples of ratios of adults and young as reported for various dates. The seasonal decline in number will be elaborated further in the discussion of life equations.

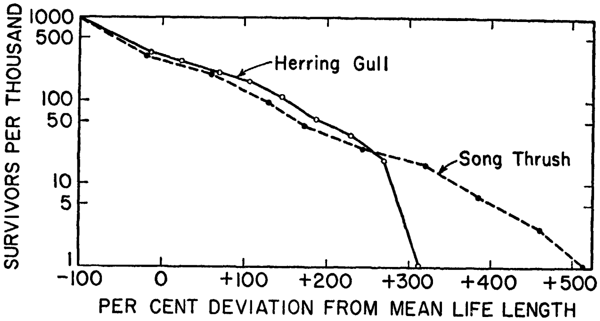


Fig. 8·1. *Survival in the Herring Gull and Song Thrush. The data for Gulls represent survivors per thousand hatched, for the Thrush, survivors per thousand adults. (After Edward S. Deevey, "Life Tables for Natural Populations of Animals,"* Quarterly Review of Biology, *22(1947):283–314.)*

The death rate of adult birds appears to be fairly constant (Fig. 8·1). For the American Robin, it is said to be about 52 per cent a year. For the Mourning Dove, it is estimated to be 80 per cent the first year and 55 per cent a year for the next 10 years. But on the average, the death rate may be about 45 per cent for each age class.

Life tables have been used commonly in the study of human mortality rates, but only a few have been attempted for birds. Various starting dates have been used, but the January 1 following hatching is suggested as best. Life tables have been given by Deevey (1947). Table 8·4 shows a representative life table for the Herring Gull. The life expectancy in years after August 1 has been reported for several species: Lapwing, 2.36; Herring Gull, 2.44; English Blackbird, 1.58; Song Thrush, 1.44; English Robin, 1.01; Starling, 1.49.

Age Indicators. Birds have a determinate type of growth which renders difficult the telling of age, but some useful indicators are available for bird study. The *skull* in young Passerine birds, for example, requires about 6 months for complete ossification, so that the

Table 8·4

Life Table for the Herring Gull, Based on 1,252 Birds Banded as Chicks at Kent Island, Bay of Fundy, 1936–1945

Age (Years)	Age as Per Cent of Deviation from Mean Length of Life	No. Dying in Age Interval per 1,000 Hatched	No. Surviving at Beginning of Age Interval per 1,000 Hatched	Mortality Rate per Thousand Alive at Start of Age Interval	Expectation of Life or Mean Life Time Left to Those Reaching Age Intervals (Years)
0–1	−100	419	1,000	419	2.44
1–2	− 59	181	581	312	2.84
2–3	− 18	95	400	238	2.90
3–4	+ 23	65	305	213	2.65
4–5	+ 64	69	240	288	2.22
5–6	+105	60	171	351	1.92
6–7	+146	45	111	405	1.68
7–8	+187	21	66	318	1.48
8–9	+228	26	45	578	.95
9–10	+269	19	19	1,000	.53

Source: Edward S. Deevey, "Life Tables for Natural Populations of Animals," *Quarterly Review of Biology*, 22(1947):283–314.

skulls of young birds in summer or early fall have a clearer and softer appearance than those of adults. Later this gives way to the granulated and hard appearance of the adult. A Passerine skull with incomplete ossification indicates a bird of the year.

The *bursa of Fabricius* can be used until about midwinter (sometimes longer) for separating old and young gallinaceous birds, Waterfowl, and probably some others. The bursa usually has disappeared or become closed in adults, while that of the young remains open and measurably deep (Fig. 8·2). The bursa may close in late summer among Passerine birds. The *spur* of birds like the Pheasant requires time to develop and is smaller in the younger birds. The *bill* of the young Woodpecker feels noticeably sharper against the hand than that of an adult which has been dulled by chisel-work.

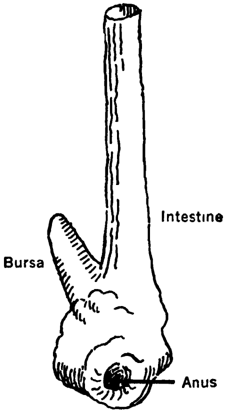


Fig. 8·2. *The bursa of Fabricius disappears in adults and for many birds can be used to indicate age. (By permission from* The Ducks, Geese, and Swans of North America, *by Francis H. Kortright. Copyright, 1942, American Wildlife Institute, Washington, D. C.)*

Young birds have plumages somewhat fluffier than adults, but it may take considerable experience to recognize the difference. Some birds have immature plumages which last beyond the first year. The Bald Eagle, for example, takes at least 3 years and perhaps 4 or 5 years to obtain its white head and white tail. Obviously, therefore, a Bald Eagle without the white head or tail would be less than 3 or 4 years of age and one with it would be more. In the same way, the plumage of the Herring Gull requires 3 to 4 years for complete development. The plumage of each year's age class differs somewhat from that of others, so that by careful study a Herring Gull population could be divided into one, two, and three, or even older age groups with considerable accuracy. We readily recognize the plumage of first-year birds like the American Robin, American Egret, and Red-winged Blackbird. Sometimes remnants of immature plumage persist 2 years or more, as in the Rose-breasted Grosbeak, Crossbill, Purple Finch, and sometimes in the Redstart. Young birds may retain a few juvenile feathers, e.g., the vestiges of crossbars or edgings in primary coverts of the Mourning Dove, Bob-white, and Hungarian Partridge (Fig. 8·3).

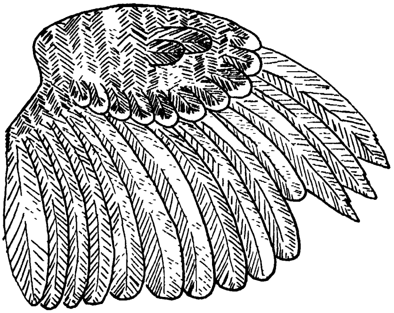


Fig. 8·3. *The edgings on the wing coverts of this Bob-white indicates a bird of the year.*

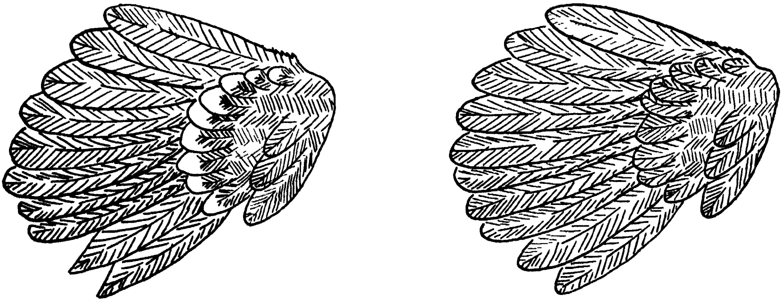


Fig. 8·4. *The outer two juvenile primaries of gallinaceous birds are retained until the first postbreeding molt, which indicates a young bird (right).*

Primaries usually molt from the inside outward and secondaries from the outside inward (Chapter 7). Since molt is generally progressive, tables and charts can be constructed to indicate age during the first summer by progress of wing molt. The ninth and tenth primaries (outer) of young gallinaceous birds are carried through to the following fall, while all those of adults are replaced in the same molt, so that young birds in the fall and spring have wing feathers of two different plumages. The ninth and tenth primaries represent the juvenile plumage and the rest represent the first-winter plumage. The two outer primaries of the young look more pointed and worn than the primaries of adults, which character is useful as an indicator of age until the fall of the year following hatching (Fig. 8·4).

The *flight* and *tail feathers* of young Ravens and Crows and perhaps all members of the Corvidae do not molt the first fall. The tail and wing feathers thus will appear more worn in first-year birds and will have a brownish cast rather than the glossy black of the adult.

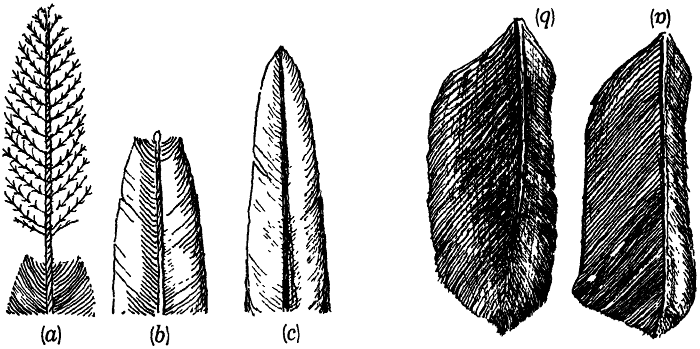


Fig. 8·5. Left. *The down of some Waterfowl (a) breaks off to leave a notch (b) that indicates a young bird in contrast to the adult tail feather (c). (By permission from* Ducks, Geese, and Swans of North America, *by Francis H. Kortright, p. 26. Copyright, 1942, Wildlife Management Institute, Washington, D. C.)* Right. *The irregular wear and shape of the outer tail feather of the young Crow (b) contrasts strongly with that of the adult (a). (After J. T. Emlen, Jr., "Age Determination in the American Crow,"* Condor, *38(1936):101.)*

The wing length of adults is also greater than that of the young. The ventral ridge of the barbs lacks pigmentation in the young as compared with those of the adult. The ventral part of the rachis of the wing feathers is whitish nearly to the tip in first-year birds. The tail itself appears rounded in first-year birds but the tail of second-year birds has a squarish appearance (Fig. 8·5.).

The *down feather* in Waterfowl, as in other birds, grows from the same feather follicle as the succeeding feather, which carries the down feather on its tip as it pushes out. In the tail of Waterfowl, the down breaks off and leaves a notch, often easily recognized, which denotes a bird of the year (Fig. 8·5). The tail and wing feathers of the young have a dull appearance also.

The *feet* and *legs* of adult Pigeons and Doves bear heavier scales than those of young birds; the feet of the young also have a pinkish appearance. The feet and legs of older Mallards, Shovelers, Black Ducks, and Mergansers are brighter red than those of the young. The undersurface of the claws in very young Crows has a horn color.

The color of the *iris* may at times be usable for distinguishing age, although we know comparatively little about the color of the iris, just as we know little about many other color characters in birds. The iris in very young Crows is blue; it is yellow in the adult Eagle but brown in the young.

Poultry handlers have developed a rapid technique for distinguishing the sex of day-old chicks by inverting the cloaca to show the *genital eminence* in the male chick or its absence in the female. Skilled operators can sex upward of a thousand an hour with better than 95 per cent accuracy. With practice, the technique may be applicable to nestling birds.

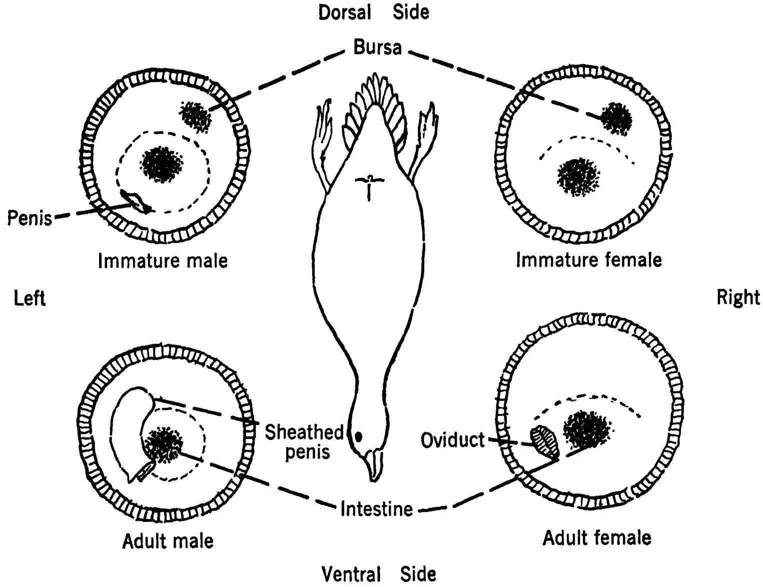


Fig. 8·6. *The presence of a sheathed penis indicates an adult male in the Waterfowl. The visible opening to the oviduct indicates an adult female. The bursa of Fabricius indicates a young bird. (By permission from* Ducks, Geese, and Swans of North America, *by Francis H. Kortright, p. 35. Copyright, 1942, Wildlife Management Institute, Washington, D. C.)*

Adult Waterfowl can be distinguished from the young by the sheathed penis of the adult male and prominent oviducal opening of the adult female. This will indicate sex at the same time (Fig. 8·6).

The *bill* in male Red-winged Blackbirds may be used also as an indicator of age. The young have a short and stubby bill which grows longer with age (Fig. 8·7). Because the bill of these birds has been used also as a taxonomic character, only birds of the same subspecies can be used comparatively for age determination.

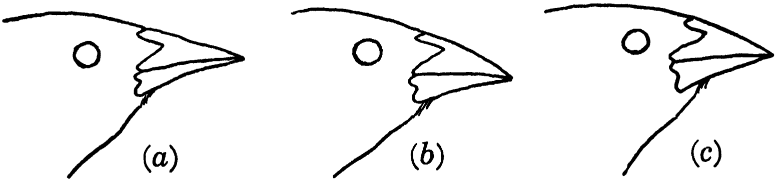


Fig. 8·7. *Age variation in the Nevada Red-winged Blackbird. (a) Adults, (b) one-year old, (c) juvenile. (After A. J. Van Rossem, "The California Forms of* Agelaius phoeniceous *(Linnaeus)*," Condor, *28(1926): 215–230.)*

Young of the California Gull have a black bill that becomes progressively yellower as the bird matures. It takes about four years to reach the adult stage of a yellow bill with a small red spot on the upper and lower mandibles (Fig. 8·8). Changes in the Herring Gull are similar.

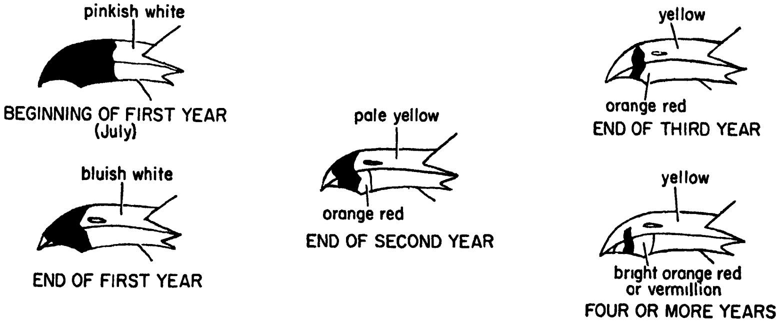


Fig. 8·8. *The bill of many Gulls varies with age, as shown in these diagrams of the bill of the California Gull. (After David W. Johnson, "The Annual Reproductive Cycle of the California Gull,* Condor, *58 (1956):134–162.)*

SEX RATIOS

A large assemblage of information on sex ratios of game birds has already been accumulated; these data suggest widely different variations in time, place, and species (Mayr, 1939). In theory, at least, the *primary sex ratio* (at fertilization) is equal. Should there be no differential mortality in the oviduct or during incubation, the *secondary sex ratio* (at hatching) should also be equal. Were there no differential mortality in life, the *tertiary sex ratio* (postnatal) would also be equal. The secondary sex ratio in most birds may show a slight excess of males, a condition paralleling that for mammals. The ratio for the Domestic Fowl is given as 97:100.* We must consider the whole matter of bird sex ratios as subject to very great error. Some indication of the ratio of males to each one hundred females appears in Table 8·5.

Table 8·5

Reported Ratios of Males to One Hundred Females

Species	Ratio	Species	Ratio
	PRIMARY RATIO		
Boat-tailed Grackle	44	Herring Gull	106
	SECONDARY RATIO		
Boat-tailed Grackle	52	Mallard	111
Rock Dove	105	Pintail	134
Domestic Fowl	97	Canvas-back	103
	TERTIARY RATIO		
Boat-tailed Grackle	53	American Crow	124
European Blackbird	67	Mallard	109
Song Sparrow	105	Pintail	55, 288
Chiff-chaff	177	Baldpate	114
Starling	212	Canvas-back	85, 195
Bob-white	114	Dabbling Ducks	111
American Goshawk	61	Diving Ducks	161
Eastern Cowbird	248	New World Warblers (average)	119
Valley Quail	112	Mourning Dove (adult)	128
Mourning Dove (immature)	113		

Observations indicate some consistent variations, though we cannot interpret their entire significance. Studies of Waterfowl indicate that males consistently outnumber the females. Much variation among species and among various groups of the same species in different areas has been reported. But studies of sex ratios in broods seem to indicate ratios more nearly equal than in adults. They suggest either a rather higher mortality ratio among females or important geographic segregation. The hatching ratio of the Canvas-back in Manitoba, for example, has been reported as 103 males to each 100 females. But male ratios of 195 (spring, Manitoba), 85 (spring, Manitoba), 85 (fall, Manitoba), 210 (Washington), 450 (Louisiana), and 205 (Louisiana) indicate the very real difficulty of determining the true sex ratio of so wide-ranging a bird (Yocom, 1951).

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* One method of indicating sex ratio is as a ratio of males to a hundred females, which method is used here.

The Honey-eater family (*Meliphagidae*) has a genus (*Myzomela*) of the Australian region in which the males outnumber the females by reported numbers varying from about 105 males to each 100 females to more than 1,000:100. A related genus (*Lichmera*) is reported to have males outnumbering the females 8 or 9 to 1 (Mayr, 1939).

Variations in sex ratio may have some correlations with the life history of the species, but evidence of such relationship has not been developed satisfactorily. Concerted effort over the whole range of a species whose sex may be readily recognized in the field, coupled with consistent local counts of adults and young, seems essential for picturing sex ratios adequately.

SUGGESTED READING

*ALLEN, ARTHUR A., *The Book of Bird Life*. New York: D. Van Nostrand Co., Inc., 1930.

*ALLEN, GLOVER H., *Birds and Their Attributes*. Boston: Marshall Jones Co., 1925.

BROWN, C. EMERSON, "Longevity of Birds in Captivity," *Auk*, 45(1928):345–348.

FLOWER, STANLEY SMITH, "Further Notes on the Duration of Life in Animals—IV Birds," *Proceedings of the Zoological Society of London*, Series A (1938):195–235.

MAYR, ERNST, "The Sex Ratio in Wild Birds," *American Naturalist*, 73(1939):156–179.

MITCHELL, P. CHALMERS, "On the Longevity and Relative Viability in Mammals and Birds, with a Note on the Theory of Longevity," *Proceedings of the Zoological Society of London* (1911):425-458.

RICHDALE, L. E., *Sexual Life of the Penguins*. Lawrence, Kan.: University of Kansas Press, 1951.

RICHDALE, L. E., *Study of a Group of Penguins of Known Age*. Dunedin, New Zealand: Privately published, 1939.

9

Evolution in Bird Life

We can hardly discuss the relationships of any species or its environmental adaptations and distribution without frequent reference to evolution. Indeed, even interpretation of behavior in the individual often requires reference to the workings of evolution. The scarcity of birds in the fossil record precludes demonstrations of relationships, changes, and trends such as have been made with some mammals and reptiles. But the large fund of knowledge of living birds (larger by far than the corresponding knowledge of other groups) lays before the student a great array of evolutionary results. These illustrate well many of our concepts of evolution and evolutionary processes as they operate in the living animal. Especially is this true of nonstructural characters, which have attracted the attention of field students.

Evolution has been defined as slow, inheritable changes through successive generations. The fewer the number of generations between animals and their common ancestor (or perhaps more correctly their common ancestral population), the closer do we consider the relationship. But because this relationship cannot be established by counting generations, as in the family relationships of man, naturalists customarily use degrees of difference and similarity as indicators of relationship (Chapter 2).

EVOLUTION OF STRUCTURE AND HABIT

Characters Undergoing Evolution. Although all inheritable characteristics of a bird are subject to modification, evolution apparently has not followed all the avenues theoretically open. Some characters have received considerably more evolutionary attention than others. The trend in the Galliformes, for example, seems to have been for greater selection of terrestrial characters and that of the Anseriformes for improved aquatic adaptation. It would be theoretically possible for some gallinaceous line to have evolved in an aquatic direction and for some Anserines to have taken on gallinaceous habits. (The terrestrial habits of some, such as the Nene Goose (Hawaii) or the Falkland Goose, can hardly be called true gallinaceous traits.) The restriction of the evolutionary range to certain lines in various species or groups has been explained by mutations in genes, the genes perhaps being chemical substances limited in their reactions by molecular structure. Such chemical limitations would thus determine the subsequent range of variation expressed by the characters under genetic control. But a fundamental weakness (and to some nongeneticists an insurmountable flaw) in the evolution-by-mutation concept is the field and laboratory evidence that mutations are well-nigh universally of a weakening nature adversely affecting vigor (page 395).

However evolution may be controlled or induced, any character influenced by one or more genes could conceivably evolve into something else. Evolution may involve structure, physiology, behavior, or any other inherited trait. Evolved characters may not now appear of an adaptive nature, though characters we recognize as being of "survival value" do. (Subjectiveness is involved, however, in our recognition of adaptiveness and survival value.) In a sense, various species of birds are not necessarily so well adapted to their respective positions in nature as might be the case (Chapter 3). The assumption that characters evolve for greater "biological efficiency" may not be true always. Anyone who has watched a male Scissor-tailed Flycatcher flying in a wind alongside a female can readily see the greater handicap provided by his tail (Fig. 3·7). In the same way, a male Boat-tailed Grackle is no aerial match for the female or even for other Grackles. Such characters may have evolved for purposes other than everyday living. Adaptations may be for different aspects of life: what may be an advantage in one aspect may be a minor detriment in another.

But many birds appear to get along well even though not perfectly adapted; yet lack of critical adjustment seems to spell extinction. In a sense, we measure successful adaptation to environment by survival and by the number of descendants produced, in the latter cases preferably perhaps on a *biomass* basis. But this may not be altogether sound; were we able ~~to measure the~~ biomass (page 256) on the basis of ecological occupation, we would probably be on sounder grounds. A grassland bird found to occupy 90 per cent of its available living space might be considered proportionately more successful than a more numerous brushland bird occupying but 70 per cent of its living space.

The great bill of Toucans seems to have no "adaptive explanation," and it may doubtfully suggest one of the lines of evolutionary effort open in the Toucan inheritable make-up that has been persistently followed (Fig. 9·1), perhaps as an avian example of *orthogenesis*. While it seems to be a rule that characters not of survival value tend to drop out, it may be that "neutral" characters like the unusual Toucan bill do not follow such a rule. We must recognize, however, our incomplete knowledge of the relationship of the Toucan bill to the bird's total behavior pattern. Like the tail of the male Scissor-tailed Flycatcher, it may serve as a social releaser.

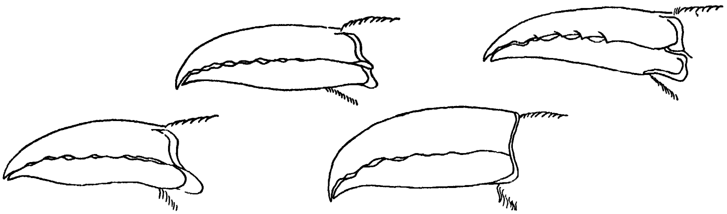

Fig. 9·1. *The great bills of the various Toucans have no recognized adaptive character for everyday living. Their excess development (hypertely) may be related, however, to some such function as social releasers.*

Adaptations and Evolution. The adaptive nature of bird life forms one of the marvels of natural history, and the preservation of common traits in related birds, which they no doubt have inherited from common ancestors, forms still another marvel. Volumes have been written on these two subjects, but many are the pitfalls besetting our thinking on the subject of survival and adaptation. The greatest loss of the bird population is in the young, and characters deemed "adaptive" by biologists seldom are those of the young. Yet to say that a character has a survival value need not necessarily imply natural selection at work (Chapter 3). Additionally, there may be no such thing as "nonadaptive variation"; our lack of knowledge may be responsible for the idea.

The selective action of the environment determines which inheritable variations survive. Two trends may be recognized in this selective process: change of the species with time, and increase in the number of species in space. In a sense, bird evolution is a process whereby those most efficiently adapted to use the biological energy in the environment prosper at the expense of less efficient ones (page 199). It must be recognized, however, that changes in the environment may result in additional and other evolutionary readjustment in organisms.

Birds having genetic traits differing from others within a species may evolve along separate lines through the workings of *isolation*. The large number of island forms testifies to the effectiveness of geographic isolation in concentrating variations and bringing about recognizable taxonomic differences. Isolation may take forms other than geographic separation; ecological isolation seems to be rather common and probably a factor in evolutionary changes. The greater variation toward the periphery of a species range probably reflects both geographic and ecological influences. *Reproductive isolation*, however, by whatever means accomplished, is the ultimate isolation.

Evolution in the More Recent Past. The similarities of skeletal structure between Miocene and Recent birds are remarkable (Howard, 1947). There seem to have been no great changes in bird life, except extinction of species, for a long time past. The evolutionary trend since the Pleistocene shows consistent characteristics in some groups. In the Pleistocene deposits of the famed Rancho La Brea (which deposits may have had selective action), only about 10 per cent of the birds represented are reported to be of extinct species, in contrast to more than 40 per cent of the mammals. The ratio of the extinct to the living in the predatory birds, on the basis of numbers of individuals, is 23.8 per cent; in mammals the ratio is 95.1 per cent (Howard, 1930). More than half the fossils belong to families of the Falconiformes (Fig. 9·2).

The fossil record indicates that the time since the Pleistocene (and probably Pleistocene also) has been a period of little evolution of species. But in passing such judgment upon recent evolution, one should not overlook the short span of geologic time involved. The Pleistocene and Post-Pleistocene times, however, seem to have been periods of considerable extermination of bird life. About 15 per cent of modern North American species are already known to have lived in the Pleistocene. It seems likely that all species of today were here then, along with many no longer present. It is suggested that all in all, a much richer bird fauna may have existed in those earlier days (Wetmore, 1933). Yet bird distribution has clearly changed; only in 8,000 of the past 80,000 years have there been any arboreal birds north of Germany (Moreau, 1954).

Among the birds becoming extinct in the Pleistocene or since are some of more than usual interest. The giant condor-like *Teratornis merriami* is known from the California and Florida deposits. At least one extinct Turkey (*Meleagris tridens*) lived along with the modern Turkey, but we do not know what constituted their respective habitat requirements. We should, of course, expect northern birds to move equatorward with the advance of the continental ice

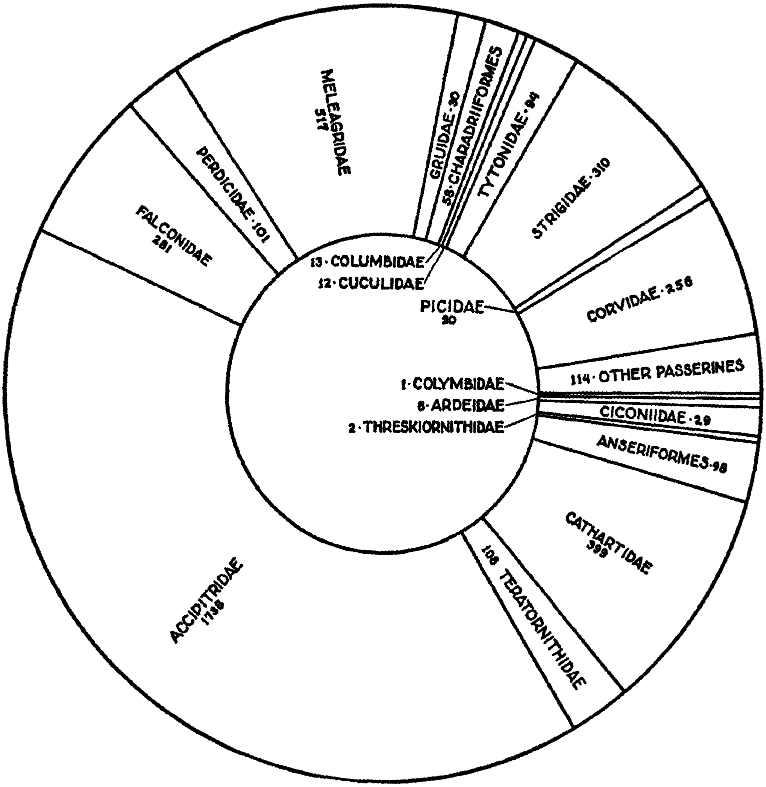

Fig. 9·2. *The relative abundance of individuals in each family of birds recorded from the Rancho La Brea deposits of the Pleistocene. (After Hildegarde Howard, "A Census of the Pleistocene Birds of Rancho La Brea from Collections in the Los Angeles Museum,"* Condor, *32(1930): 81–88.)*

cap. Yet many birds now found farther south lived in the southern states. In the Florida Pleistocene deposits, for example, are found bones of the Jabiru, Mexican Turkey, and Wood-rail, none of which now ranges that far north. The California Condor also reached Florida and probably had a continuous range between Florida and the West Coast.

Behavior Evolution. There can be no doubt that behavior characteristics have evolved just as have structural ones. The fact that members of a group, such as genus, family, and even order, have characteristic behavior patterns shows the influence of evolution (see

Chapter 10). Many of these are adaptive in nature, but others do not appear so on the basis of our present knowledge, except perhaps in a general way.

Members of the Holarctic Paridae use variations of a call recognized in its best-known rendition as *chick-a-dee*. Yet the Paridae, from the survival standpoint, seem no better off with this type of note than the Fringillidae with their *chip*! or the soft Parulidae *tsip*. The need for a distinctive species call-note is self-evident, but it could take many forms, and the similarity within the family can be interpreted reasonably as evolutionary modifications of an ancestral call. In the same way, the Paridae live in the woods and only a few have radiated into other habitats; the family association with forest is quite likely an ancestral one.

The rather more plastic Fringillidae (see Table 9·1) show marked preference for brushy areas or ecological substitutes. But within the family, adaptive radiation has superimposed upon the presumable ancestral trait modifications that mask the original. Evening Grosbeaks prefer large timber and large timber tracts, as do also the Crossbills. Most members of the subfamily Carduelinae, to which these belong, show the same trait, and from this we can postulate that a common ancestor (or ancestral group) evolved the habit and passed it on down through its descendant species. In like manner, the Richmondeninae subfamily has its characteristic habitat selection, largely tall brush. The third subfamily, Emberizinae, largely stays with the brush—or its ecological equivalent, heavy herbs; some have come to prefer short trees and some rather open grass areas. The trait has become almost lost in some like the Vesper Sparrow, which, even though it nests on the ground, prefers hayfields, cropland, and fence rows but eschews large fallow fields.

Prey Selection. The selection of prey by avian predators illus~~trates the workings~~ of adaptive survival and other processes. It has been shown that, under experimental conditions (page 78), Owls catch mice concealingly colored significantly less often than those not so well matched to the background (Dice, 1945b, 1947). The Owls most capable of catching concealingly colored mice would appear to have the best survival chances, just as the least conspicuous mice would also. We can logically expect that concealing coloration operates in the case of small bird prey as it does for mice and in the case of other predators as it does with Owls.

Coloration of Young and Nest. An ingenious ornithologist studying ~~birds in the dry Great Basin~~ noted the tendency of the nestling down to be light or dark according to nest site and for the nest lining to vary somewhat the same way, though the latter was not so clearly evident (Fig. 9·3). This relationship is explained as a device combining habit and structure to protect the young from sunlight (though it could be explained also as protective coloration). The lighter down and lighter nest lining of the species having exposed nests reflect the solar rays and thereby aid heat toleration. Species that live under darker or less exposed conditions have dark down and dark lining, which enable them to absorb and take advantage of the sun's warming rays.

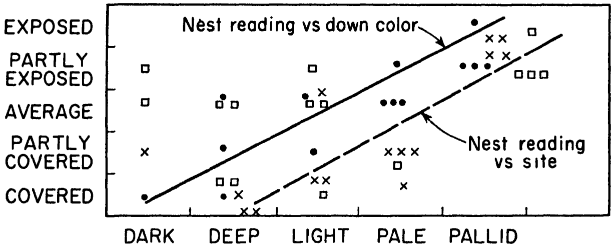

Fig. 9·3. *The nest lining of exposed nests tends to be lighter than that of covered ones. The data are from fifteen different species of birds. (Adapted from data by Jean A. Linsdale, "Coloration of Downy Young and of Nest Linings,"* Condor, *38(1936):111–117.)*

The two responses indicate habit evolution in the adult, which selects the nest site and the nest material, and structural evolution in the young, which grows the down. A combination of adult and young evolution is involved. In some species other ways of counteracting harmful heat rays have been noted, chief among them shielding the young with the body of the parent. In such cases, however, down and nest lining do not necessarily show lightness with increased exposure.

EVOLUTION AND ECOLOGICAL FACTORS

Evolution and Ecological Stress. It seems entirely plausible that world periods of great stress, particularly climatic, should be periods of great evolutionary activity. The fact that the bird's feather covering and constant body temperature make it possible to inhabit cold regions without hibernation may have reduced the importance of stress periods as compared to other animals. In the same way, the body covering may protect also from tropical heat and sun so that—anomalous though it may be—birds have become well adapted to heat and cold by the same insulating feature.

An ecological condition favoring bird evolution is the presence of suitable *niches* into which a bird may move by evolutionary adaptation. It is suggested that when two species meet in the same area, individuals that vary most from the general type have a selective advantage, particularly if the difference is in feeding structures or in habits. This suggestion has been invoked to explain the evolution of island birds after invasion, such as of the Hawaiian Honey-creepers, as well as in other types of island bird life (Amadon, 1947). Successive invasions of an area by the same species may establish additional species if the invasions are far enough apart in time so that descendants of previous invasions have evolved into distinct and separate species. But if the invasions are too close, the interchange of genetic characters, through interbreeding, will prevent evolution into new species.

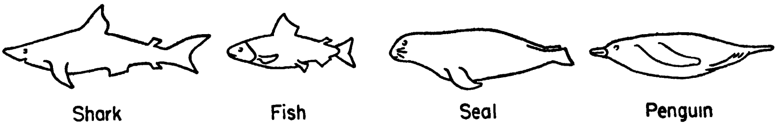

Fig. 9·4. *Penguins (and* Hesperornis*) of the bird world show adaptive convergence for marine life as in seals and other oceanic vertebrates. They have the streamlined bodies and paddle-like limbs of swimming vertebrates.*

Isolation has had marked influences in the bird world, an example being the Penguins (page 37) of the Southern Hemisphere (Fig. 9·4). But isolation does not always favor the bird. About 97 per cent of the forms becoming extinct in the past two centuries lived on islands, which have been said to serve as areas of genetic selection and as evolutionary traps. Some 18 per cent of the natural avifauna of Hawaii has been reported as extinct and about 11 per cent of that in New Zealand. But the only evidence that these extinct birds were out of adjustment with their times came after man's interference. The assumptions of ornithologists, therefore, may be open to some question.

Evolutionary Succession. That birds have risen and fallen to extinction in the past seems axiomatic. Excellent studies of the Rancho La Brea remains show the succession in the Cathartine dynasty (Fig. 9·5). Vultures live today, three species in the United States and Canada and three in Central and South America. The fossil record testifies to the principle of *racial senescence.* In the Pleistocene, the modern Black and Turkey Vultures were ascending in abundance and distribution (which is still going on) and the Condor already declining. Several other species became extinct before the Pleistocene and

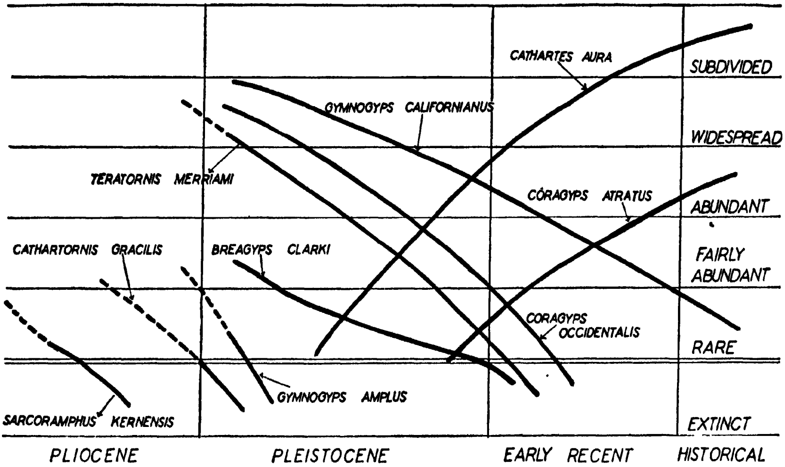

Fig. 9•5. *Succession in the Cathartine dynasty showing abundance and geologic history of the Cathartine Vultures. (After Loye Miller, "Succession in the Cathartine Dynasty,"* Condor, *44(1942):212-213.)*

a few persisted almost to historical times. A phylogenetic tree showing the probable relationship among the Vultures in another manner is given in Fig. 9·6.

Ecological Habits and Species Formation. The Blue Grouse of western North America has developed into two groups of subspecies, a coastal (*fuliginosus*, *sierrae*, and *howardi*) and an interior one (*obscurus*, *richardsoni*, *flemingi*, and *pallidus*). The birds winter in the high country and descend to lower levels for breeding; only along summits as in the Cascade Mountains do the two groups come into contact. With the coming of spring, each descends its own slope for breeding (page 297), so that each is isolated from the other. Were it their habit to ascend in the summer and descend in winter as customary for other animals, such isolation would not occur. Hence, two different species may be in the making, just as others have developed in the past (Fig. 9·6).

An overcrowded population suffers from intraspecies competition ~~and st~~rife, which does not appear necessarily to be in the best interests of the species, even though it does influence the survival rate and in that way perhaps contributes to evolutionary effort. "Underpopulation," on the other hand, has unfavorable social influences, and these also may bear upon the survival rate. It seems possible that an undercrowded organism (if such ever occurs except temporarily) or one in small and scattered numbers must face a rather vigorous environ-

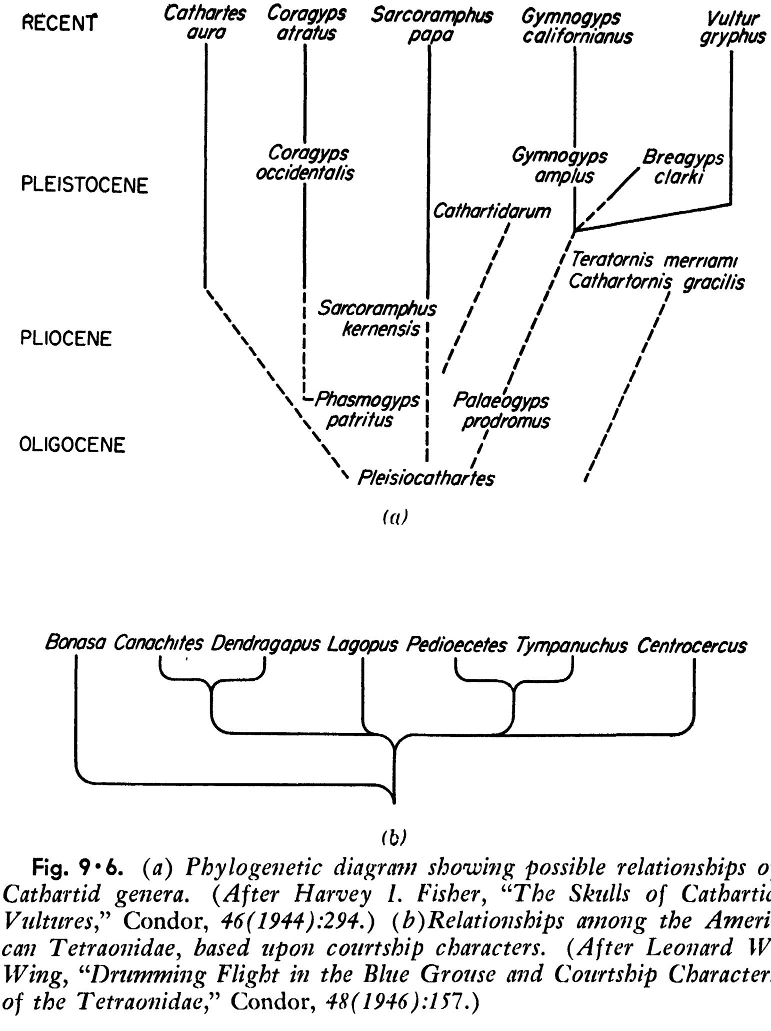

Fig. 9•6. (*a*) *Phylogenetic diagram showing possible relationships of Cathartid genera. (After Harvey I. Fisher, "The Skulls of Cathartid Vultures,"* Condor, *46(1944):294.)* (*b*)*Relationships among the American Tetraonidae, based upon courtship characters. (After Leonard W. Wing, "Drumming Flight in the Blue Grouse and Courtship Characters of the Tetraonidae,"* Condor, *48(1946):157.)*

mental life if it is to progress. The rigors of life may act in this case as a molding force, just as crowding may among dense populations.

VARIABILITY

The newly hatched bird does not resemble its parents except in a general way and must go through a developmental period, occasionally of several years, before it does match its parents. Many of our commonest birds, even the male House Sparrow in our streets, take on a winter plumage differing from that of the summer. Acquisition of a bright breeding plumage is a fairly common practice. The white plumage worn by the Ptarmigan in winter differs more from the gray or brown of the summer than from parallel plumages of other species of Ptarmigan.

Many of the variations involving the individual will be considered in Chapter 20, which treats of heredity in the bird world (see also Chapter 10). But whether these inheritable variations will become stamped upon the population character is said to be governed in part by restrictions on the flow of genes between adjoining bird populations. Birds isolated, as on islands, or restricted in their movement, as in isolated habitats, or of low mobility may concentrate a genetic character differing from their neighbors and so become marked groups (though not necessarily of taxonomic standing).

Some very interesting evolutionary variations have occurred in many parts of the bird world. The Ptarmigan of the Scottish moors (known as the Red Grouse) no longer changes to a white plumage in winter, though its relatives do. In Australia and the neighboring islands, variations in the plumages of males and females occur in the Flycatcher, *Petroica multicolor.* In Australia and Tasmania, males and females wear different plumages characteristic of the sex; the sexes are alike in Samoa but the plumage is typical of the male in the other areas; in part of the New Hebrides, however, the plumages are still alike but the plumage is one like that of the female elsewhere.

Some habits may be explained better as traditional rather than hereditary. *Tradition* may be defined as a habit passed along from generation to generation by association. Though migrating south in the fall is an inherited trait, we may consider it traditional for the Whooping Crane to winter on the Aransas Peninsula in Texas and to stop in migration at certain places along the Platte River. Each young bird has learned of these two places by accompanying its elders. In the same way, Falcon eyries and even Tit nesting holes have been occupied by successive pairs of birds year after year for more than a century. The later occupants, however, were far removed in time from the first ones. It has been reported that Peregrine Falcons still nest on ledges from which falconers obtained birds in the Middle Ages.

Continuous and Discontinuous Variation. Few species live as one continuous group; the majority have been shown to break up into races and sometimes into *species groups.* In the same way, there are few species without some geographic variations of habit, song, or behavior. No doubt many hidden variations exist also. In a sense, a species consists of a "collection of populations."

Variations occur more in discontinuous ranges than in continuous ones, but all ranges are in a sense discontinuous, for they are formed of occupied habitat scattered through an uninhabited matrix. The ocean is more uniform than terrestrial habitat, for example, and its major groups have fewer species and races. The small populations of isolated islands make possible rapid turnover and mixing of the entire gene complex and thereby greater uniformity than elsewhere. An island population may have started from only a few individuals and embrace but a portion of the whole genetic variability of a species.

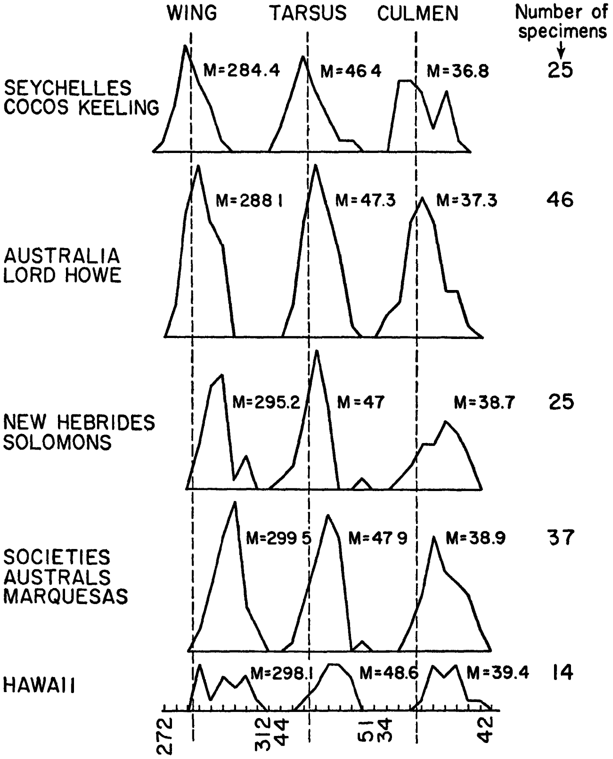

Fig. 9·7. *Cline of increasing size from west to east in ten populations of the Wedge-tailed Shearwater as expressed by frequency distribution graphs. Dotted line represents means of wing, tarsus, and culmen in Indian Ocean populations. There is a gradual increase in average dimensions of birds from the Seychelles to the central Pacific. (Adapted from Robert Cushman Murphy,* The Population of the Wedge-tailed Shearwater, *p. 5. American Museum of Novitiates, No. 1512.)*

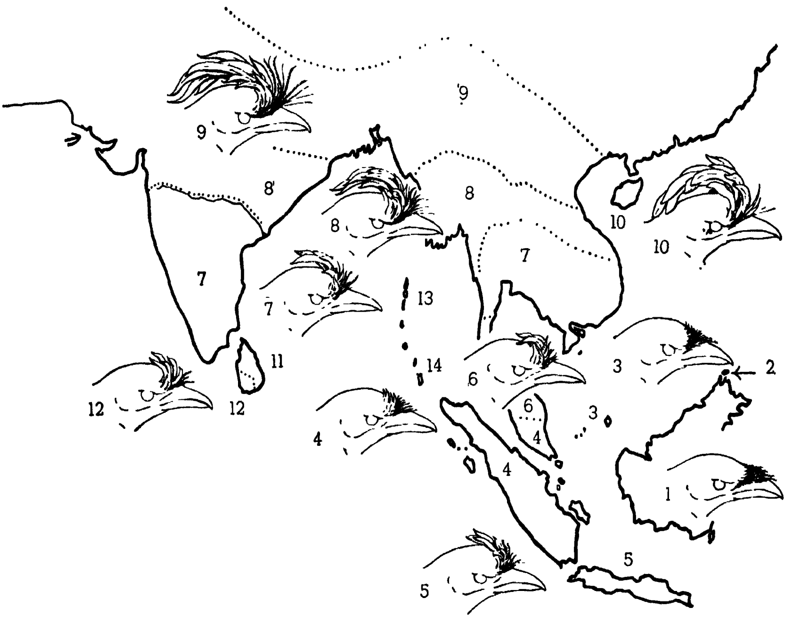

Fig. 9·8. *The head adornment of the Drongo* (Dicrurus paradiseus) *of southeast Asia shows every variation from no crests to long crests. Note increase from the small Bornean subspecies (1) to the large Himalayan one (9).* (*1*) Brachyphorus, (*2*) microlophus, (*3*) platurus, (*4*) formosus, (*5*) hypobellus, (*6*) paradiseus, (7) rangoonensis, (*8*) grandis, (*9*) johni, (*10*) lophorinus. (*From Ernst Mayr and Charles Vaurie, "Evolution in the Family Dicruridae (Birds)*," Evolution, *2(1948):238-265.*)

A continuous variation, such as the south to north increase in body size or body proportions, is termed a variation gradient or cline (Fig. 9·7). Continuous variations of a quantitative nature most commonly are ones such as pigmentation, size, relative proportion of body parts, and physiological responses. In the Drongo (*Dicrurus paradiseus*) every stage is found between uncrested subspecies at one end and crested forms at the other (Fig. 9·8).

The tendency of many birds to behave somewhat differently at the *periphery* of the range from those in the heartland probably reflects discontinuous variations. Often the same trend occurs in poor habitat within the heartland. Thus, well-situated Mockingbirds in the heartland do significantly less mimicking of their fellow birds than ill-situated ones or those of the periphery. The Chat of the periphery shows markedly more shyness and retiring habits than those of the main range (Brooks, 1942). Brewer Sparrows occupy the sagebrush in parts of the West, but elsewhere they are birds of the brushy roadsides, pastures, and even timberline shrubs.

The variability of habit along the periphery or edge of the range seems to parallel other variations to some extent. Striking subspecies occur mostly at the periphery of a species range rather than at the center (Mayr and Vaurie, 1948). It is said, however, that in any major group of organisms, we should look to the point of origin for advanced present-day types rather than for primitive present-day ones (Murphy, 1936).

Variability of Domestic Birds. The very great variability of domestic birds indicates the biological possibilities of selection, artificial though it is. A "breed" actually represents a homogeneous gene complex, and perhaps two hundred breeds of domestic pigeons exist, all descended from the Rock Dove (*Columba livia*) of southeastern Europe and Asia Minor. There are recognizable breeds of Chicken, many of bizarre appearance, far different from the ancestral Jungle Fowl. One of the most unusual of the breeds is the Silky Fowl, so named because its plumage appears soft, as though covered with a silklike hair. The barbules of the feathers are not provided with barbicels, or they are so much reduced that the feather does not consolidate as in the normal Chicken. All the contour feathers seem to be either retained down or contour feathers much changed from the normal. But such a character in the wild Jungle Fowl would seemingly be a most unfavorable one for survival.

Flightlessness. Although the central evolutionary effort of birds has been for flight and great modification of structure, physiology, and behavior to go with it, some birds have lost the power of flight. We can conceive of the flight evolution of birds as leading into a niche occupied by the rather inefficient flying reptiles that had to give way before the onslaught of the more efficient birds. Because air-borne life takes a high degree of specialization, it is not to be wondered that birds still dominate it, whereas the land-bound reptile gave way on land before the mammal that could compete better with only a slightly improved biological efficiency. But just how the initial aerial movement of the bird succeeded in the face of the pterodactyls that we assume may have dominated the sky is difficult to perceive. We may presume that the initial approach to aerial life was along lines more efficient (or climatically independent) for the bird than formerly as well as more efficient than those of the flying reptile. Birds probably preyed upon the smaller dinosaurs from the air, and perhaps the young and eggs of larger ones, which would assist mammals and climate in bringing on reptilian downfall. Yet the flying reptiles may not have dominated the aerial zone and the attributes that go with it in sufficient degree to close all possible niches.

The large *Diatryma* of the Miocene shows that even in the past the aerial bird had reinvaded the earth-bound realm otherwise left to the mammal (Fig. 9·9) just as the flightless *Hesperornis* invaded the marine realm earlier. But flightlessness seems to confer no special favors upon the possessors, and flightless birds seem to have traveled into an evolutionary box canyon compared to their flying relatives. Flightless birds are few and none has widespread distribution today. The insular and distributionally remote regions of Australia and New Zealand are the homes of the flightless Kiwi, Notornis, Emu, and Cassowary (Fig. 9·9).

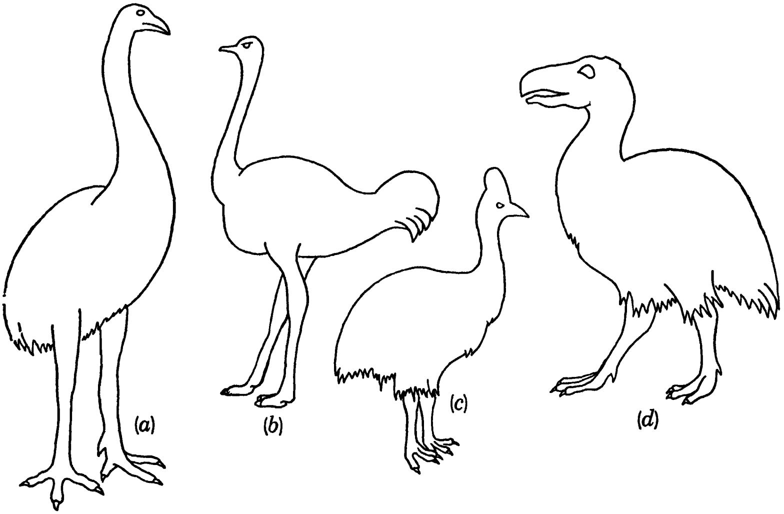

Fig. 9·9. *Several giant flightless land birds have lived.* (*a*) *Moa* (*recently extinct*), (*b*) *Ostrich* (*living*), (*c*) *Cassowary* (*living*), (*d*) *Diatryma* (*Miocene*).

Flightlessness may arise in almost any group where the inability to fly is not a current disadvantage (Fig. 9·10). The Burrowing Parrot (*Strigops*, or sometimes *Stringops*) of New Zealand has almost no keel, so long has it lived flightless. In the Alcidae, the Great Auk survived before man destroyed it; its range, however, could hardly be called remote from land masses. On the Galapagos Islands occurs a flightless Cormorant at the northern range limit of the flightless Penguins. A flightless Rail, now extinct, lived in the Laysan Islands and a flightless Wren in the West Indies (Baldwin, 1947). The flightless Grebe reported from Lake Titicaca in South America is assumed to have arrived as a flier at some remote period in time.

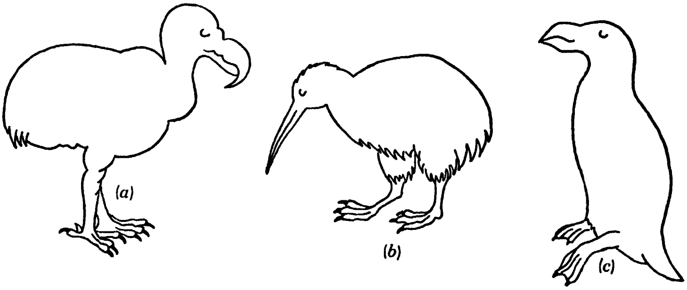

Fig. 9 • 10. *Flightlessness may occur in isolated groups or remote places where loss of flight appears to confer no fatal disadvantage for the time being under natural conditions.* (*a*) *Dodo* (*Columbiformes*), (*b*) *Kiwi* (*Apterygiformes*), (*c*) *Great Auk* (*Charadriiformes*).

EVOLUTION AND DISTRIBUTION

Evolution and Adaptive Radiation. Many groups of birds show rather unusual capacities for adapting themselves to various ecological conditions. In fact, active adaptive radiation seems almost like a characteristic of some. Yet some show little tendency for becoming adapted to several differing ecological situations (Fig. 9·11). Several members of the same family will often penetrate the same type of environment; members of several different families may also penetrate the same type (Table 9·1). Thus, the forest may be the home of birds that belong to such families as Strigidae, Tetraonidae, and Fringillidae. Members of these same families occur also on treeless tundra. They have thus made parallel penetrations of these major ecological types. Birds are particularly noted for this habit (Fig. 9·12); other animals may do so but not so conspicuously. Because of *convergence*, the resulting, unrelated birds may on occasion appear more alike in looks and actions than other more closely related ones. They may become *ecological homologues* (page 35).

At times, adaptive radiation appears to become a high specialization that may indicate racial age (irrespective of the number of calendar years involved). Among living birds are some characteristics that have sometimes been interpreted as indicating racial old age. The

Table 9·1

Parallel Family Penetration of Major Types

Family	Hardwood Forest	Conifer Forest	Dry Brush	Wet Brush	Prairie	Steppe	Tundra	Marsh	Desert
Tetraonidae	Ruffed Grouse	Blue Grouse	Ruffed Grouse	-	Prairie Chicken	Sharp-tailed Grouse	Ptarmigan	-	Sage Grouse
Fringillidae	Rose-breasted Grosbeak	Junco	Cardinal	Swamp Sparrow	Dickcissel	Vesper Sparrow	Snow Bunting	Song Sparrow	Desert Sparrow
Turdidae	Wood Thrush	Hermit Thrush	Veery	-	-	-	-	-	-
Parulidae	Ovenbird	Myrtle Warbler	Chat	Yellow-throat	-	-	-	Yellow-throat	-
Strigidae	Barred Owl	Long-eared Owl	-	-	Short-eared Owl	Burrowing Owl	Snowy Owl	Short-eared Owl	Elf Owl
Buteonidae	Broad-winged Hawk	Goshawk	Sharp-shinned Hawk	-	Swainson Hawk	Ferruginous Rough-leg	American Rough-leg	Marsh Harrier	Prairie Falcon

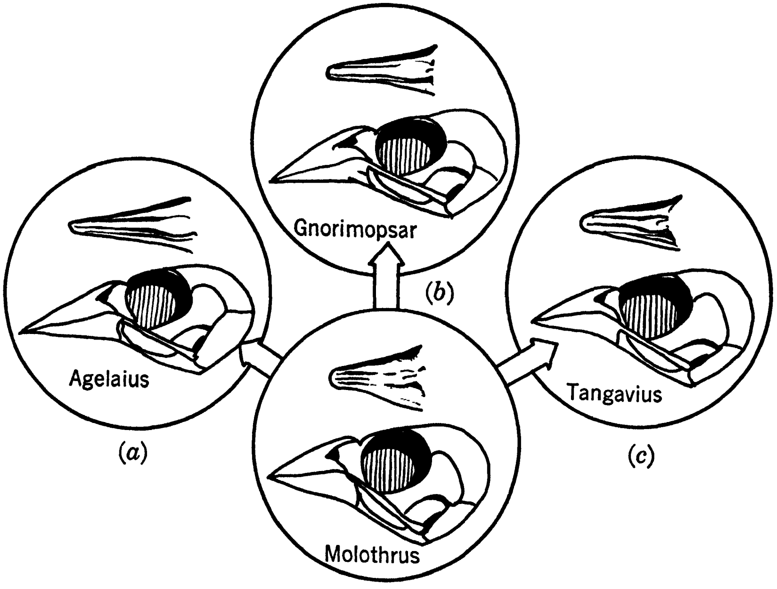

Fig. 9·11. *Possible origin of the three major icterid lines from an ancestral Cowbird: (a) Blackbird-Troupial (agelaiine), (b) Grackle (quiscaline), and (c) Cacique (cassicine) lines. (From William J. Beecher, "Adaptations for Food Gathering in the American Blackbirds,"* Auk, *68(1951):411–446.)*

Kirtland Warbler, for example, has become so particular in its wants as to occupy a very restricted habitat in a very restricted range. In its special adjustment for feeding extensively upon bark beetles, the Ivory-billed Woodpecker may show equal restrictiveness. Though we can perhaps think of these species as "old," it does not necessarily reflect family "senility." The Wood Warblers (Parulidae) surely are a "vigorous" family: the Black and Turkey Vultures are also vigorous, though the California Condor is not (Fig. 9·5); most Woodpeckers would clearly be considered as vigorous species, even though the Ivory-billed may be thought otherwise.

Evolution and Spread. The relation between evolution and distribution reveals many workings of evolutionary processes, as is illustrated by the various Chickadees of western and northern North America (Fig. 9·13). The Chestnut-backed Chickadee occupies the humid Pacific Coast region from the Alaskan panhandle south to Monterey, California, in a narrow strip usually fewer than a hundred

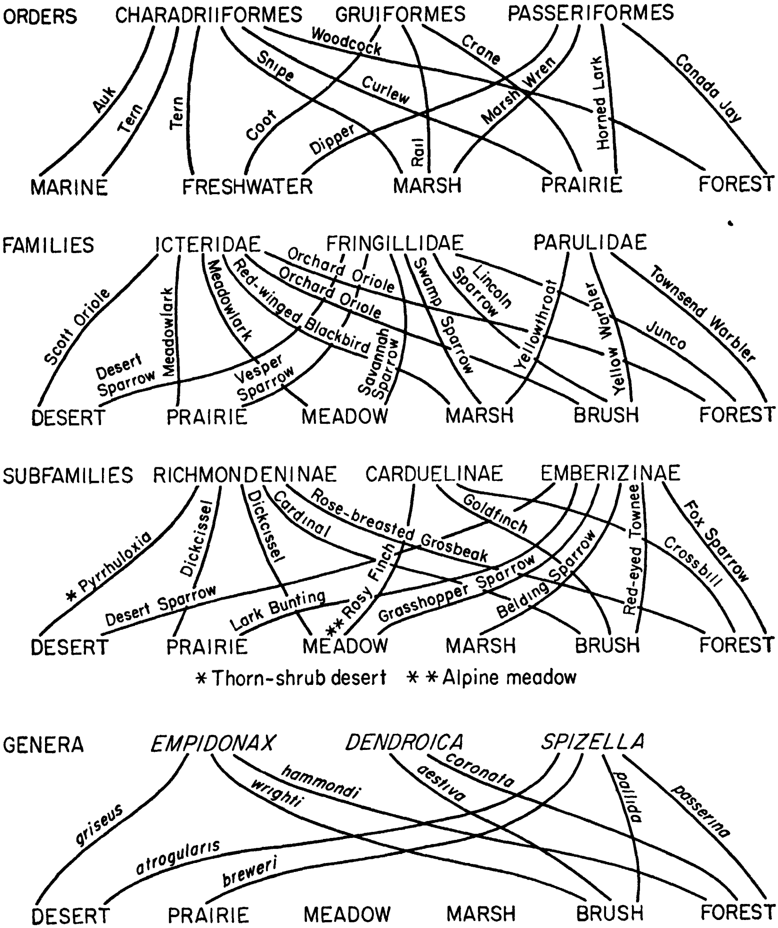

Fig. 9 · 12. *Adaptive radiation results from the evolutionary invasion of habitats as illustrated by competitive radiation of various groups into common habitats. The larger groups radiate most widely. Genera seldom use more than two or three different general habitats, and species seldom use more than one.*

miles wide but extending into northern Idaho and adjacent Montana (Grinnell, 1904). To the north, the Hudsonian Chickadee has its breeding range across northern North America south to the United States border. The Alaskan Chickadee lives in the Alaskan region and adjacent Canada.

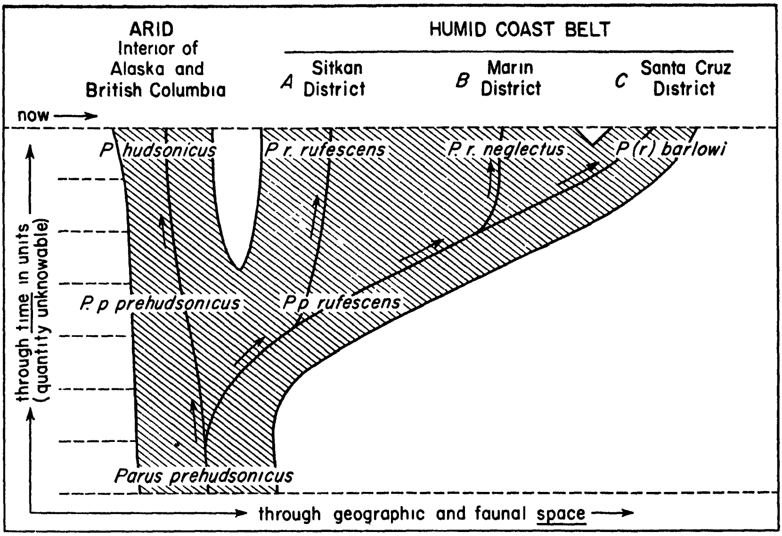

Fig. 9 • 13. *Evolution and spread of the Chickadees of western North America. (After Joseph Grinnell, "The Origin and Distribution of the Chestnut-backed Chickadee,"* Auk, *21(1904):364–382.)*

Certain characteristics of these birds are apparent. The young Hudsonian resembles the parents, while those of the Chestnut-backed resemble the presumed general ancestral type more than today's adults. The sides of all are rusty when young, though those of *Parus rufescens barlowi* are gray when adult, those of *P.r. neglectus* pale rusty when adult, and those of *P.r. rufescens* deep brown in adulthood. The young of *P.r. barlowi* are paler than those of the others. The difference in adults follows the *Gloger Rule* of paler color in drier areas, darker in more humid ones. *P.r. rufescens* occupies the humid coast, *P.r. neglectus* the fairly humid Marin district, while *P.r. barlowi* lives in the drier Santa Cruz country. In general, *Parus rufescens* differs from *Parus hudsonicus* by intensification of browns and decrease of size under conditions of moist climate. The Chestnut-backed Chickadees pushing farther down the coast have become lighter again in the drier climate (Grinnell, 1904).

In addition to color differences, the Hudsonian Chickadee has a shorter tail, which is in line with the rule of shorter tails for birds of the tree tops having more powerful flight than those of the bushes and lower tree branches. The Hudsonian occupies the tops of trees and lives in taller trees more. (In the same way, Mockingbirds, Bush-tits, and Wren-tits that flit from limb to limb or from bush to bush across short open spaces have developed relatively long tails.)

Among naturalists, the term *endemic* is sometimes used in referring to birds now living in the place of evolutionary origin. The difference between *native* and *endemic* (the latter may have a different use in medicine) is that a species is native to a place that it occupies by its own efforts as distinguished from occupation resulting from acts of man. The bird may have evolved at some distance and have spread at some time in the geologic past. Thus, two species may be native to the same island, but the ancestors of one may have come from the mainland, those of the other became a species (or subspecies) on the island. The latter would be called endemic.

SUGGESTED READING

DOBZHANSKY, T. G., *Genetics and the Origin of Species*. New York: Columbia University Press, 1941.

GRASSE, PIERRE-P., *Traité de Zoologie: Oiseaux*. Vol. 15. Paris: Masson et Cie, 1950.

GREGORY, WILLIAM K., *Evolution Emerging*. New York: The Macmillan Co., 1951.

HEILMANN, GERHARD, *The Origin of Birds*. New York: Appleton-Century-Crofts, Inc., 1927.

MATHEW, WILLIAM DILLER, *Climate and Evolution*. New York Academy of Sciences, Special Publications, 1939.

MAYR, ERNST, *Systematics and the Origin of Species*. New York: Columbia University Press, 1942.

MAYR, ERNST, E. G. LINDSEY, and R. L. USINGER, *Methods and Principles of Systematic Zoology*. New York: McGraw-Hill Book Co., Inc., 1953.

NEWMAN, H. H., *The Phylum Chordata*. New York: The Macmillan Co., 1939.

*PYCRAFT, W. P., *A History of Birds*. London: Methuen & Company, 1910.

*THOMSON, J. ARTHUR, *The Biology of Birds*. New York: The Macmillan Co., 1923.

*SIMPSON, GEORGE GAYLORD, *The Major Features of Evolution*. New York: Columbia University Press, 1953.

10

Bird Distribution

Like so many other matters of nature, bird distribution is a continuous process. We can see it today largely as an end product from the past, save for what may happen in the short span of an observer's lifetime or that of the written word. In addition to the natural distribution, an acceleration of change has been brought about by the impact of man himself upon the earth. To the findings of living distribution may be added fragments of fact from findings in the fossil and subfossil record.

For the sake of brevity, the many factors influencing the distribution of birds may be listed as *ecological* and *historical* ones. The ecological factor includes both the suitability of the habitat (obviously, it must be suitable else the species will not prosper) and the development of the environment that makes it suitable (that is, *ecological evolution*). The historical factor includes both the development of the bird that it may become adapted to a habitat (*organic evolution*) and development of the land and its attributes (*physical evolution*). Ecological evolution depends to a high degree upon physical evolution (and sometimes *vice versa*). That they overlap or merge is another example of the oft-stated axiom that nature shuns disjunction.

ZOOGEOGRAPHIC FACTORS AFFECTING DISTRIBUTION

Needs of a Species. Biologists conceive of each species as possessing combinations of needs peculiar to itself and distinct from those of every other species. Except for geographical restrictions, such as those of islands, the range of each species of bird differs from that of all others. And except for possible obligate parasites, the range for each species differs from that of all other animals also.

Although birds by their warm-blooded nature are able to live somewhat independent of temperature, the prime element that still controls their distribution is a suitable climate. Other needs center around such characteristics as cover and the physical make-up of the environment, but no doubt many subtle needs also exist. In a sense, *cover* is partly an expression of climate, and the most important influence of climate on birds seems to be this indirect one through cover. The physical character of the cover in part reflects the topography. All in all, so intertwined are these needs of a species that we cannot arbitrarily delimit them, but we can recognize their operations by field evidence.

An adjustment in the respective abilities and adaptations of the Prairie and Peregrine Falcons illustrates the presence of determining factors in the selection and maintenance of their respective ranges in western America.* Both species have about the same size wing and body, but the Prairie Falcon is lighter in weight than the Peregrine. Hence, it has a lower wing-load and consequently greater advantage in the thinner air of higher altitudes. The Peregrine is a water bather, the Prairie a dust bather, which ties the Peregrine to water and aids the Prairie in using dry regions. Both feed upon birds caught in fair flight, but the relatively greater power of the Peregrine, because of greater muscle-to-wing ratio, makes it superior in lowland bird pursuit. The Prairie, however, feeds upon rodents far more than the Peregrine, an adaptive adjustment to the dry regions, the lands where rodents are most abundant. The accuracy in flight of the Prairie Falcon defies description. A ground squirrel peeking out of its burrow may have but an inch of head exposed as it surveys the outside, but this is a sufficient target for the full-power stoop of a Prairie Falcon. The open talons hit the target, the rear toe being the principal weapon with the forward talons coming into play like a pair of tongs. They hold and bear off a light rodent, but they tear through a heavy one, which often lands mortally wounded away from its burrow, in position for a return pickup. This coordination for pin-pointing its target at high speed may be equally developed in the Peregrine—as anyone might agree who has seen one capture a White-throated Swift—but the Peregrine seldom stoops to rodents or birds on the ground. Although a few Peregrines nest above 5,000 feet altitude and a Prairie Falcon nest has been reported on an island in the Gulf of California, the balance in their respective capacities and needs is such that the Peregrine generally occupies the humid regions, shores, and lowlands. The Prairie Falcon, on the other hand, takes over the dry regions and high altitudes. Slight variations in habits and capacities between other closely related species may likewise be found.

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* Dr. R. M. Bond has kindly supplied much of this information from his unpublished and matchless field observations of Falcons.

A brief survey of the Cliff Swallow colonies in the Sacramento Valley of California showed that sixty-eight colonies containing some 8,200 birds occupied about 1,600 square miles, the closest colonies being scarcely a half mile distant (Emlen, 1941). All used man-made structures (bridges and buildings) though in nature the species uses cliffs, usually along streams but always near to water. The main requirements for a nesting site in this case seem to have been a protected vertical surface, reasonably open terrain, and a nearby mud supply.

Zoogeographic Laws. The recognized laws of zoogeographic distribution may be stated briefly as follows: All animals are found wherever conditions are suitable unless (1) they were unable to reach an area, (2) they reached an area but were unable to survive, or (3) they reached an area and evolved into another species. These three principles of animal distribution show clearly in bird life even though birds, because of their flight power, have greater mobility than other vertebrates.

What appears to be a case of inability to reach suitable range occurred in the distribution of the Mountain Quail in the Pacific Northwest. The indications are that originally it reached north only as far as the Columbia River, and that settlers in the region moved some birds to the Washington side about the year 1860, where they have since succeeded well. It would appear that the width of the lower Columbia River exceeded the flight limit of the bird. Island birds as a rule belong to groups on the nearby mainland. Only the strongest flyers generally have the power to reach the more distant islands. Flight powers and flight limits, it should be self-evident, form one of the limitations to spread.

The second principle has been shown a number of times, though chiefly through the fossil records. Trogons now confined to the Old and New World Tropics once ranged as far as France in the Old World and no doubt occupied the land between. Fossil Condors in Florida and fossil Albatrosses in England show wider former distributions for these species than is seen now, and evidently they were unable to stay after having once become established. Even the excursions of the Dickcissel into New England and its subsequent retreat show evident inability to survive. Dickcissel remains in an Indian Pueblo of the twelfth century (Miller, 1940) suggest that once the species may have invaded the Southwest (Fig. 10·1).

The third rule, that of evolution into another form, appears frequently. Thus the Black-capped Chickadee is believed to have become transformed into the Carolina Chickadee in southeastern North America, just as the Hudsonian probably gave rise to the Chestnut-backed (Fig. 9·13).

Members of the Tetraonidae seem able to show all three rules in operation, as do members of most other families. The members of the Brush Grouse group (*Bonasa*) have not been able to spread into the Old World because no suitable brush connection seems to have extended across the Alaska-Siberia land bridge.* But Tundra Grouse (Ptarmigan) have crossed over the tundra connection. Members of the Tree Grouse group have made the crossing, clearly when timbered conditions were more favorable than at present. The Spruce Grouse crossed at some time in the recent past and became *Canachites* (*Falcipennis*) *falcipennis*. But the Prairie Grouse have not crossed; they are birds chiefly of dry interior grasslands, and any coastal grassland in Alaska would probably have been a marine type, humid and unsuitable. The Ptarmigan once covered many mountain tops of

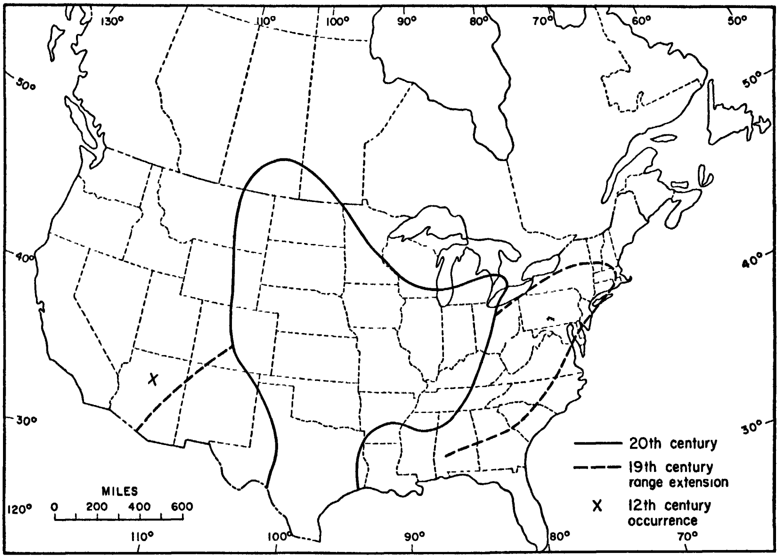

Fig. 10·1. *The range of the Dickcissel in the twentieth century includes chiefly the interior prairie country. In the nineteenth century, it reached New England. It reached Arizona (indicated by an X) in the twelfth century.*

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* The Hazel Grouse (*Tetrastes*) has been said to be related to the Ruffed Grouse (*Bonasa*), but parallel development seems a better explanation.

western North America, especially toward the more southern parts of the Rockies, Cascades, and Sierras, where they no longer persist. Part of the explanation seems associated with the northward march of climate since the Pleistocene and part to isolation of small remnants, a factor related to the climatic shift.

Barriers. Two opposite physical geographic features influence bird distribution. *Barriers* are features that prevent range extension, and *spread-ways* are the physical features that aid range extension. Tangible barriers appear on every hand. Expanses of water form a very definite barrier to land birds and to many shore and marsh ones also; expanses of land, on the other hand, form very definite barriers to waterbirds, especially to marine ones. A water gap between North and South America during much of the geologic past has prevented free passage of birds (Fig. 10·2). Other gaps have existed throughout the world in the past—even as now—though "island-hoppers" may cross them.

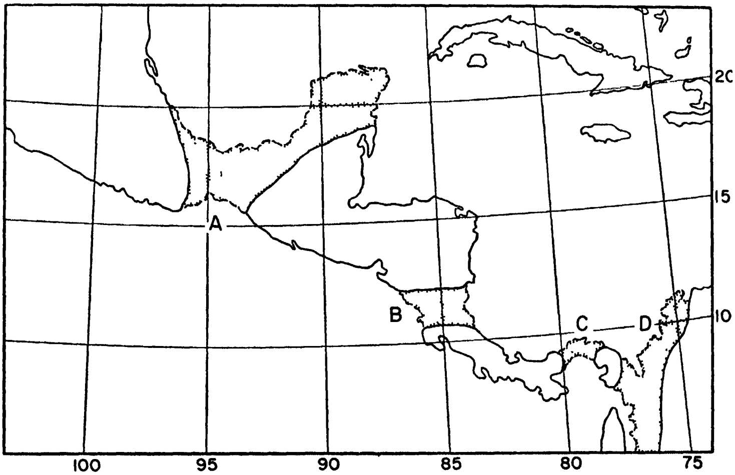

Fig. 10·2. *Tertiary water gaps have prevented free passage of birds between North and South America. (A) Tehuantepec gap (late Miocene to middle Pliocene), (B) Nicaraguan gap (late Eocene to late Oligocene), (C) Panamanian gap (late Eocene? to late Oligocene), (D) Colombian gap (middle Eocene to late Miocene). (After Ernst Mayr, "History of the North American Bird Fauna,"* Wilson Bulletin, *58(1946):3–41.)*

Grasslands serve as barriers to forest birds and forest regions to grassland forms. Even within the oceans, we find barriers no less active for some species. Birds of the cold Antarctic and Sub-Antarctic do not range far northward except along cold ocean currents, like the Humboldt, which takes the Penguin into the equatorial zone on the west side of South America.

To these barriers must be added some intangible ones, in a sense ecological, often of very great importance, though not so readily visible as the tangible ones: *zonal* (temperature, daylight), *humal* (atmospheric humidity), and *associational* (territory, food, breeding places, cover, special needs). In their northward distribution, southern birds may be limited by temperature (coolness); they meet northern birds pushing southward, also limited by temperature (warmth). Presumably, a bird can survive in a colder or hotter region than the one in which it can breed successfully, just as a planted tree may live where it cannot reproduce efficiently. In the distribution of the Chestnut-backed Chickadee, it has been shown that atmospheric humidity limits their distribution along the dry California Coast (Grinnell, 1904). Altitude plays a part, for the temperature gradient drops about 3° F. for each 1,000 feet rise of altitude.

But the associational barrier is easiest to demonstrate, though sometimes it may be the result of a zonal or humal condition. The Bobwhite seems limited northward by snow depth and snow prevalence. The Passenger Pigeon did not inhabit the West, probably because it needed hardwood that the West could not provide, and perhaps also because it nested in trees and could not spread across the prairie. The importance of suitable habitat can hardly be overestimated as an ecological need of birds. Those lacking suitable habitat or forced to establish territories in submarginal habitat have difficulty reproducing or even surviving.

Some habitat limitations are as definite as a vast ocean barrier, and a representative series of examples may not be amiss. The singing ground of a Woodcock limits it to habitat having such places. The absence of perches effectively stops the Tree Pipit, though not the Meadow Pipit. The distribution of the Oregon Jay, Rosy Finch, Kingfisher, and Meadowlark is reported to be limited in California by temperature (Grinnell, 1917). Deep snow covering its food rather than cold is said to fix the northern limit of the Carolina Wren, and the effect of summer heat determines the distribution of the White Pelican in Texas (Griscom, 1945). The Everglade Kite (page 426) does not range beyond the limits of the snail *Pomacea* (*Ampullarius*) upon which it feeds (Symposium, 1945). The lack of water restricts Valley Quail in the desert. Peregrine Falcons must have cliffs on which to nest, and Burrowing Owls avoid hard soils. A field ornithologist can readily call to mind any number of examples, and a great many have been published (e.g., Armstrong, 1947, 1950).

Pathways of Spread. Even though birds use the air freely, they require land connections for spreading outward from a center of origin. Except for island invasions, birds seem to spread by slow, amoeba-like occupation of additional range. Spread-ways may be great land bridges across which birds may pass, such as between Asia and Alaska or North and South America. They may also be local crossings. The Alaskan land bridge, when connected, helped successive waves of immigrants in both directions. Subsequent breaking of the connection gave the needed isolation for the respective populations on each continent to diverge before a reconnection of the land brought later invasions. Successive waves thus have been traced by systematists in the bird life of today.

The Central American land connection between North and South America has existed in its present form only in recent times. For most of geologic time, only a series of islands lay between the continents, which provided "stepping stones" for island-hopping invaders, though not for others (Fig. 10·2). No land bridge is known between South America and the rest of the world in avian times, so that all land birds represented in both South America and elsewhere have had to pass through North America.

It is axiomatic, however, that ecological conditions must favor a species for it to live in an area, and passage across a land bridge seems to offer no exception. Birds of the coniferous forest could hardly be expected to spread over a land bridge of tundra. Birds of the dry interiors of both Asia and America are separated now and probably have been for much of geologic time.

But barriers and spread-ways are readily apparent within land masses. No fewer than nine species have invaded the desert region as riparian avifauna along the Colorado River in the Southwest. A great forest belt sweeps across northern North America to thrust many eastern birds northwest as far as Alaska, actually west of some of their western relatives farther south. The Myrtle Warbler, Yellow-shafted Flicker, and Spruce Grouse reach places in Alaska actually west of some Audubon Warblers, Red-shafted Flickers, and Franklin Grouse farther south.

During more ancient times, a continuous environment seems a necessary postulate to account for birds of high latitudes now isolated from others of their kind. The Black-throated Green Warbler, Slate-colored Junco, and Red Crossbill of the southern Appalachians needed some such connection. The American Pipit, White-tailed Ptarmigan, Blue Grouse, and Clark Nutcracker live on isolated ranges and peaks of the Rockies, Sierras, or Wallowas, to many of which they probably spread by now nonexistent connections.

Several birds appear to be spreading northward now (perhaps but temporarily), and presumably the process as we see it here differs little from that of the past. The Cardinal, Mockingbird, Tufted Titmouse, House Finch, Carolina Wren, and Red-bellied Woodpecker of America; and the Rook, Blue Tit, Goldfinch, Firecrest, Gray Wagtail, and Lapwing of Europe show this northward trend (Fig. 10·3).

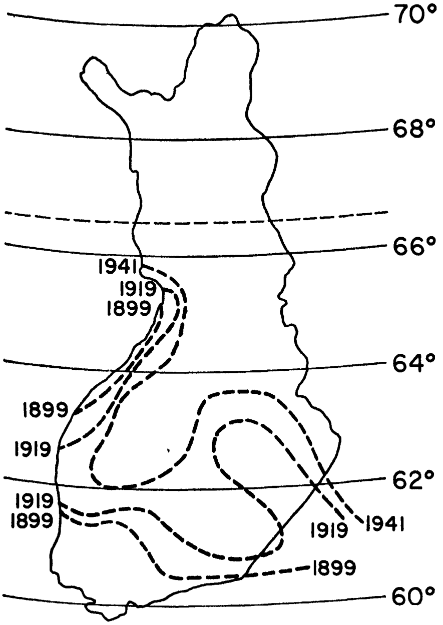

Fig. 10·3. *Extension of Lapwing range in Finland. (After Olavi Kalela, "Changes in Geographic Ranges in the Avifauna of Northern and Central Europe in Relation to Recent Changes in Climate,"* Bird-Banding, *20(1949):70–103.)*

But it must not be assumed that birds are always expanding their ranges or that it is always *northward.* The Great Black-backed Gull has spread *southward* along the North American Atlantic coast. The Western Kingbird, Lark Sparrow, and Lark Bunting have spread *eastward* in the American interior, whereas the Blue Jay, Baltimore Oriole, and Red-headed Woodpecker have gone westward. The range of the Dickcissel has receded from the Northeast (Fig. 10·1), while in Europe the Golden Oriole, Linnet, Bearded Tit, and Rock Sparrow have done somewhat the same thing (Kalela, 1949).

Accidental Spread. Accidental (irregular) distribution of birds occurs and theoretically could assist the spread of birds, though from a practical standpoint, the chief accidentals are strong fliers and birds in the fall of their first year. Land birds appear as accidentals out of their ranges mostly in migration seasons, but even the most sedentary birds may be transported or wander great distances. Many sea birds appear in places far distant from their normal range and sometimes far inland in the wake of storms. Tropical birds especially are prone to be moved by tropical storms that carry them northward. In general, given time enough in any area, almost any bird of nearby or not-too-distant regions will appear sooner or later (it has even been suggested that "state lists" will be the same as the A.O.U. check list at some distant, future date).

BIOGEOGRAPHIC FACTORS AND DISTRIBUTION

Biogeographic Divisions of the World. The world has been divided up many ways to show distributional principles and relationships. Though each system has many points in its favor, none follows very faithfully the facts of bird distribution. In a sense this is as it should be, for the mobility of birds makes it possible for them to pass across many barriers to other animals and to be rather independent of positional restrictions. Their feathers and warm-bloodedness make them rather free of many climatic problems. Yet for descriptive purposes, various segments of the several distributional systems are variously useful in bird work.

The orthodox and long-standing system of *Zoogeographic Realms* suggested by Wallace divides the world as follows:

1. *Holarctic* (North America, Eurasia, and North Africa), *Palearctic* (Old World north of Sahara and Himalayas), *Nearctic* (New World north of southern Mexico).
2. *Ethiopian* (Africa south of the Sahara)
3. *Oriental* (Southeast Asia)
4. *Neotropical* (New World from southern Mexico southward)
5. *Australian* (Australia and adjacent islands)

The Zoogeographic Realm system with its various modifications has many commendable features. *Neotropical*, *Nearctic*, *Palearctic*, and *Holarctic* have been used already in this book because they convey well an idea of the regions involved (Fig. 10·4).

The famed *Life Zone* concept of Merriam divides North America into transcontinental latitudinal zones based upon temperature sum-

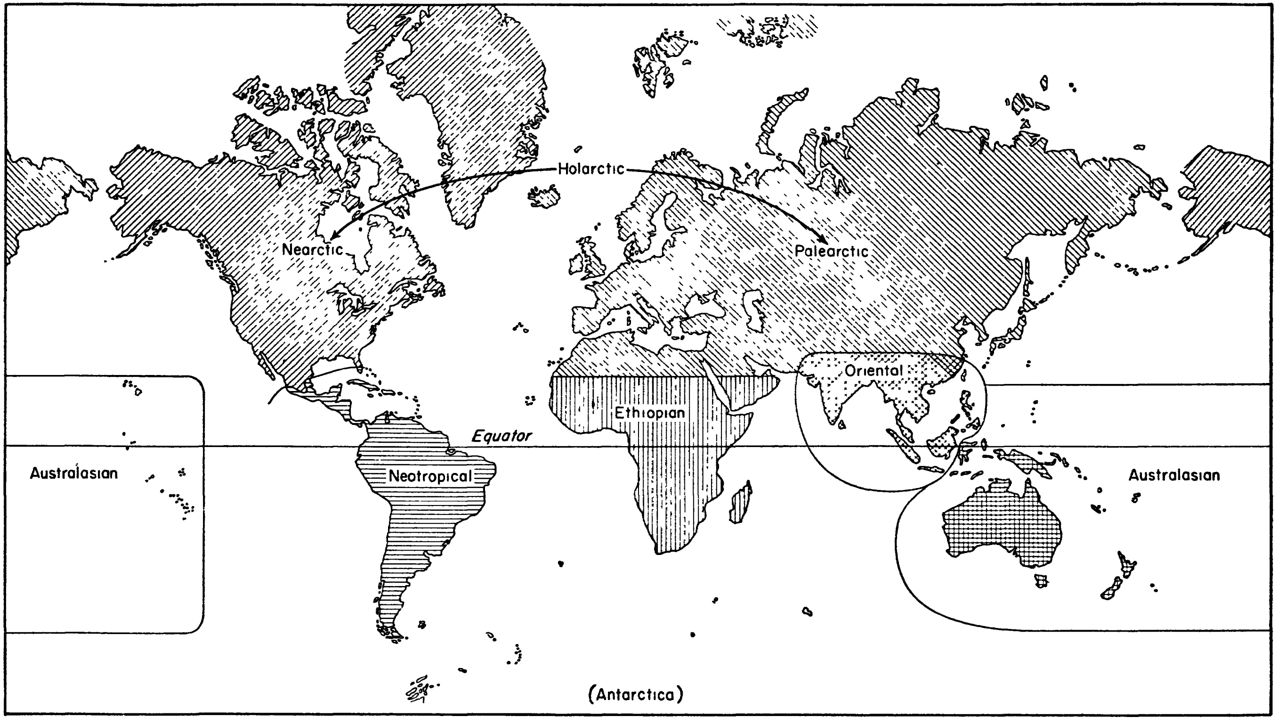

Fig. 10·4. *The zoogeographic realms. Some zoogeographers call New Zealand and Madagascar separate realms. The Palearctic and Nearctic together constitute the Holarctic.*

mations supplemented by subdivisions based upon humidity. The principal zones are:

- Boreal Region
  - Arctic Zone
  - Hudsonian Zone
  - Canadian Zone
- Austral Region
  - Transition Zone (Alleghenian, Transition)
  - Upper Austral Zone (Carolinian, Upper Sonoran)
  - Lower Austral Zone (Austroriparian, Lower Sonoran)
- Tropical Region
  - Tropical Zone

Biomes are still another representation of plant and animal distribution. (Although by definition *biomes* include animal life, they are essentially based upon plants.) The principal characteristics of the biome system are a series of large regions based upon the major features of plant distribution, which in the Holarctic world give Tundra, Coniferous Forest, Deciduous Forest, and Grassland biomes. These are climax areas—meaning permanent areas determined by climate. Intergrading areas are called *ecotones*, and there may be subclimaxes also (Pitelka, 1941). The biomes and ecotones of North America are:

- Tundra Biome
  - Tundra–Coniferous Forest ecotone
- Coniferous Forest Biome
  - Coniferous Forest–Grassland ecotone
- Deciduous Forest Biome
  - Deciduous Forest–Grassland ecotone

Birds cross all such boundaries—the American Robin alone can be found breeding in every biome and nearly all ecotones. A map of biomes and life zones will be found in *Audubon Bird Guide* (Pough, 1946).

Biotic provinces are areas rather similar in animal life, plant life, topography, and climate (Dice, 1943). They are natural regions rather readily visible to an experienced field ecologist and geographer. Biotic provinces are smaller than either biomes or life zones; some birds may cross them while others may be restricted to a single biotic province.

The governing point in bird distribution seems to be the actual condition of the habitat—*the life form*—not the major feature of the landscape. A Horned Lark uses grassland or its equivalent, whether in a prairie, a tundra, or forest region. In the same way, trees are essential to the Downy Woodpecker; these may be groves, streamside trees, or actual forest. Tall trees are not needed by the Downy; neither are closed forests. Probably bird students will find vegetation types (page 204), such as "white pine type," "poa-fescue type," "sagebrush type," "red oak type," or "dune margins," the most useful means of indicating the kind of biogeographic unit wherein particular birds may be found. These may be named on the spot when published sources are inadequate (see also Chapter 11).

Influence of Climate. As has been pointed out in the previous section, birds occupy the habitat suited to them wherever it may be found within the general limitation of climate. But the general distribution of the plants that supply the bird with its food and shelter depends upon climate.

It is entirely clear that grassland birds live wherever suitable grass conditions may be found. But the great grasslands of the world all follow a general rule: they lie on the outer borders of the drylands where rainfall effectivity is low. The general rule for drylands is that they lie in rain shadows of mountains and on the western sides of continents, bending inward and poleward from about 20°–30°

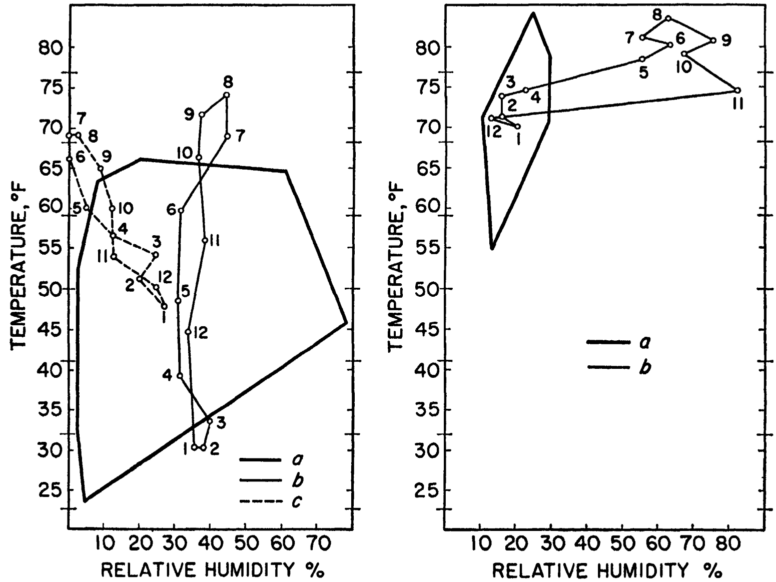

Fig. 10•5. Left. *Climograph of the Skylark in its optimum range (a) compared to Brooklyn, New York (b), and San Jose, California (c).* Right. *Climograph for the Kirtland Warbler breeding range (a) compared with the winter range in the Bahama Islands (b). The figures indicate the months. (After Arthur C. Twomey, "Climographic Study of Certain Introduced and Migratory Birds,"* Ecology, *17(1936):122–132.)*

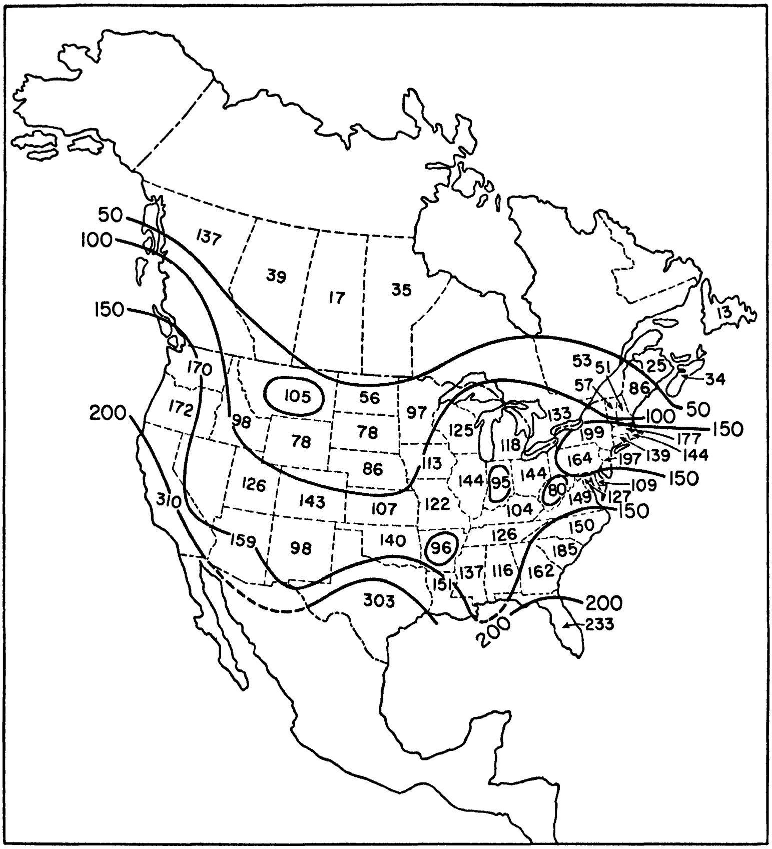

Fig. 10•6. *The winter distribution of species. Data from the Christmas Censuses, 1900–1939. (By permission from* Practice of Wildlife Conservation, *by Leonard W. Wing, p. 299. Copyright, 1951, John Wiley & Sons, Inc., 1951.)*

Latitude. Grasslands may be tropical *savannas*, *short-grass prairies* (*steppes*), or *tall-grass prairies*. In a similar general way, *conifer forests* are found where moisture is adequate and temperatures cool. (The American southern pines represent a special case of an *edaphic* nature.) *Deciduous forests* exist in humid and mid-latitudes; high temperature and rainfall in the Tropics make *rain forests*. Cold temperatures in the North result in *tundra* and at high altitudes *mountain tundra* and *mountain meadow*. Along foggy coasts may occur a special moisture-resultant flora. A *cloud forest* may exist on tropical mountain ranges where cloud moisture substitutes for rain. If rainfall is deficient, a *desert* results. Characteristic birds will be found in each of these appropriate areas.

Sometimes climate is very effective directly or in combination with other environmental factors in limiting bird life. The long cold nights of the North limit the wintering of some birds, even though their needs otherwise seem supplied just as well as farther south. The food supply and other ecological needs for the American Robin seem adequate across the southern states in summer, but the temperature appears to be too hot. A severe winter can reduce the Bob-white populations markedly in the Lake States. Humidity in the Coast Range is said to control the Gray Jay, even as it does the plant life (Grinnell, 1917).

It is true that many birds can survive beyond the limits of their natural range, even in winter; birds in zoos and captivity have shown this to be true. But *climographs* indicate that only in climates similar to the optimum are birds likely to succeed in the wild away from their native range. Climographic studies have demonstrated for some migratory birds that temperature and precipitation in the winter fall rather significantly close to the breeding optimum (Fig. 10·5). More attention needs to be given to the relative climate of winter and summer ranges of migratory birds before we can deal satisfactorily with this important matter. Importation of foreign birds has failed where the climate was unsuitable.

The winter distribution of birds by species shows a northward thrust along the coasts of North America and southward in the interior (Fig. 10·6). This is primarily a reflection of the climate, but the influence of the climate is through the winter habitat itself as well as the temperature factor.

Influence of Vegetation. The kind and quality of vegetation plays a most important role in bird distribution, and many parts of this book deal with it. One would not expect to find Meadowlarks in a hardwood forest, nor a Pileated Woodpecker out on the prairie. The Red-headed Woodpecker prefers oak trees, but the Three-toed Woodpeckers prefer conifers. Marsh Harriers may be found in large grass or grasslike areas if the vegetation is of the right height.

In dealing with bird life in the field, people unconsciously recognize the great importance of vegetation. To call a bird one of the shore, brush, or fields in a way distinguishes it on the basis of vegetation selection. Even within a single vegetation type there occur many differences of choice; one species may prefer the treetops, another the low limbs, and still another the forest floor. All correctly may be called "forest birds," but each occupies its own stratum.

Influence of Topography. The influence of topography appears most in the mountain regions, especially pronounced in such mountains as those of South America and western North America. The rise of but a thousand feet in altitude is roughly equivalent to a poleward movement of 3 degrees of latitude (Fig. 10·7). Some birds are associated with high altitudes, others with intermediate altitudes, and still others with the lowlands. The vegetation influence of topography is marked, and probably much of the topographic influence acts through vegetation. The mountain influence is more spectacular in equatorial or dry regions than in humid or high latitudes (Fig. 10·8).

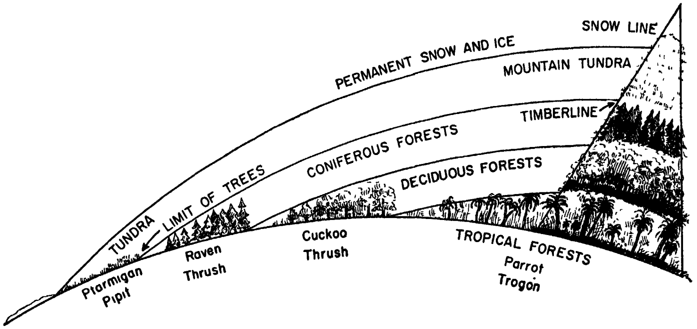

Fig. 10·7. *Comparison of the latitudinal and altitudinal zones or associations of plants providing the environments for animals.*

In addition to mountain topography, one must not overlook ordinary lowland topography—river valleys, hills, plains, and even ditch banks. Changes of topography are found wherever land varies from a flat plain. Even slight variations may change vegetation and bird life. A river bluff means home sites to Kingfishers, Bank Swallows, and Sand Martins. Often the microclimates of topography are significant in matters of bird life. Cliff Swallows may avoid hot, exposed rocks in one particular area but occupy cool, protected ones around a bend. A south-facing slope ecologically may be scores or even hundreds of miles removed from a north-facing slope which is geographically distant only a few hundred rods.

River valleys and mountain tops have opposite effects. In North America, southern birds work northward up river valleys, while northern birds persist southward along the mountain tops. Canyon Wrens, Chats and other southern birds, for example, push far up the Snake River where the adjoining hills are the home of more northern species. In the Palouse Country and other parts of the West, one

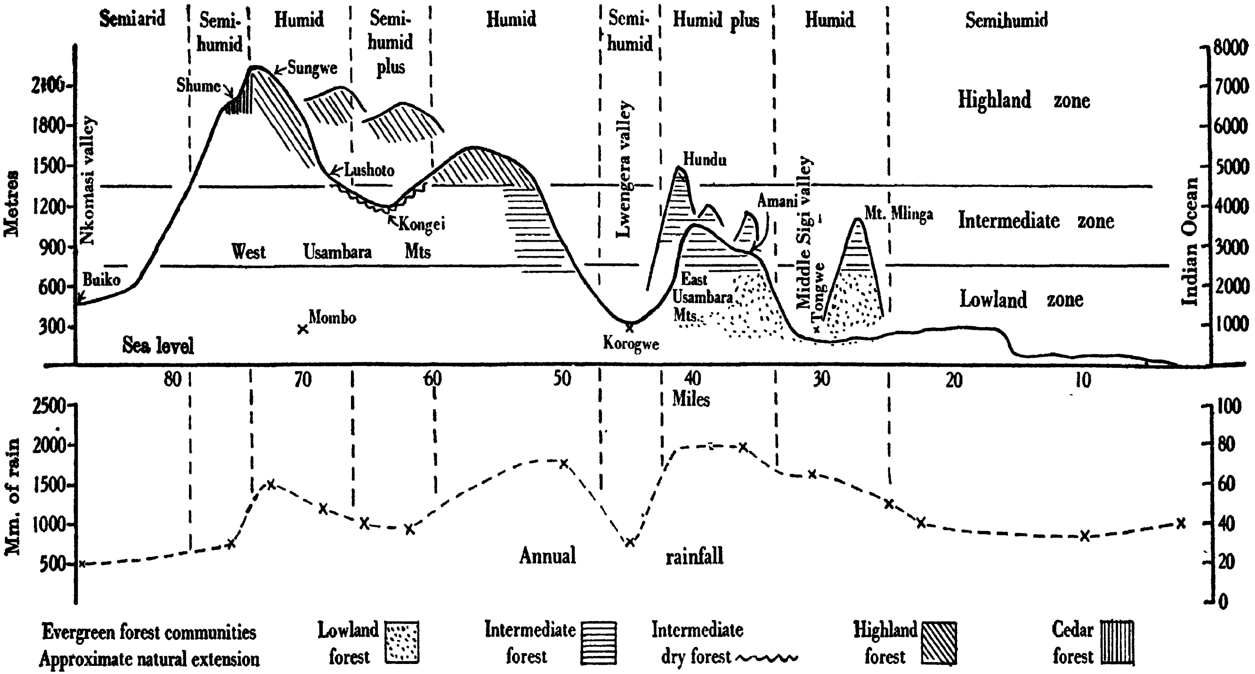

Fig. 10·8. *Diagrammatic sections of the Usambara Mountains of Africa (southwest-northwest) to show variations of rainfall, climate, and vegetation with altitude. (After R. E. Moreau, "A Synecological Study of Usambara, Tanganyika Territory, with Particular Reference to Birds,"* Journal of Ecology, *23(1935):1–43.)*

finds the Eastern Kingbird outnumbering the Western Kingbird in the hill country, but a drop of one or two thousand feet into a valley finds the reverse the case. The eastern bird favors moister hill country, the western one the drier lowland. In parts of the Cascade foothills, the Mountain Bluebird may be found at the upper end of a hill pasture and the Western Bluebird at the lower end.

Intraspecies Distribution. Certain "rules" of general application have been elaborated and may well be listed at this point.

1. Warm-blooded animals tend to become larger in the cooler and smaller in the warmer parts of the species range (*Bergmann Rule*, Table 10·1).

Table 10·1
Weight Variations (Grams) Between Cool and Warm Regions *

Species	Cooler Region	Warmer Region
Bob-white	190	160
American Sparrow Falcon	140	120
Mourning Dove	140	100
Screech Owl	180	125
Hairy Woodpecker	85	60
Downy Woodpecker	42	26
Horned Lark	43	36
American Crow	490	460
Blue Jay	88	83
Black-capped Chickadee	12	11
Tufted Titmouse	24	20
Bewick Wren	21	17
Brown Thrasher	70	56
Pine Warbler	12	11
Yellowthroat	10	9.5
Bronzed Grackle	120	108
Cardinal	44	38
Pine Grosbeak	77	57
Fox Sparrow	41	29
(Average difference, 19.9%)		

* Bird weights are relatively little known, but these are probably indicative.

Thus the Bob-whites of the South weigh about a fourth less than those of the North (Fig. 10·9A).

2. Warm-blooded animals tend to reduce projecting body parts in the colder parts of the range (*Allen Rule*). This is not well shown by birds except for such things as reduction in bill length (Fig. 10·9B), though some birds may have longer and more powerful bills for feeding on frozen ground, such as the Chough of the Himalayas (Hingston, 1926).
3. Birds of humid regions are darker than those of dry regions (*Gloger Rule*) (Fig. 10·9C).
4. Birds of cooler regions lay more eggs per set than those of warmer regions.
5. Wings tend to elongate in mountains and cold regions.

6. The races in cooler regions are more migratory than those of warmer lands.
7. Insular races have longer bills than others.
8. Birds of cooler parts of the range have longer alimentary tracts; more migratory ones have shorter cloacas (and possibly shorter alimentary tracts).
9. The more migratory birds lay eggs of greater length-breadth ratio (*Averill Rule*, page 104).

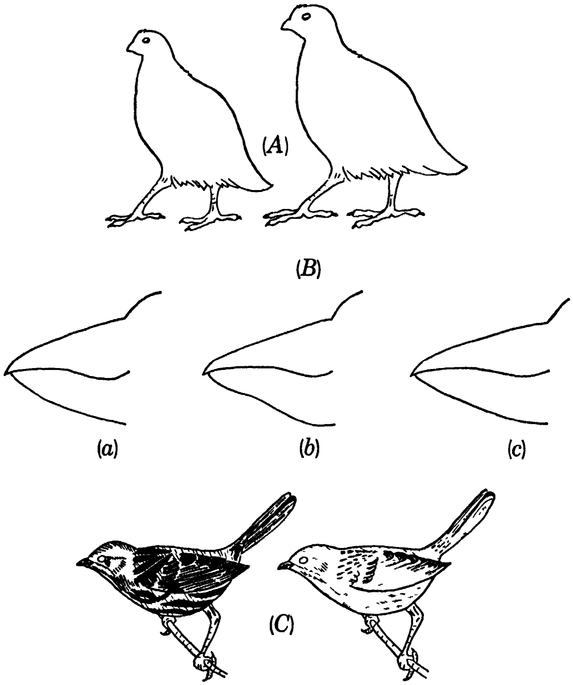

Fig. 10•9. *(A) The Bob-white of the South (left) weighs about a fourth less than that of the North (right) in keeping with the* Bergmann Rule. *(B) The bill of the Pine Grosbeak decreases northward in keeping with the* Allen Rule. *(a) Middle Rockies, (b) Canadian Rockies, (c) Alaskan interior. (C) Humid Region Song Sparrows (left) are darker than desert ones* (Gloger Rule).

Adaptability to Changed Environment. Questions of interpretation arise over the adaptability of birds to changed environment. Adaptation implies evolutionary processes, and adaptability to new environment really represents only *substitutions* of one set of conditions for others within the instinctive environmental pattern of choice.

By adaptability to changed environment we should understand *substitution ability* and *tolerance* for changed conditions.

No clear-cut principles can be drawn as yet from study of environmental changes and birds, but a few generalities have merit. Like other organisms, birds have a threshold of habitat suitability along with an upper limit of exclusion. The optimum habitat rests between (though not necessarily equidistant from) the extremes. The ecological distribution of Grouse in relation to plant succession illustrates these points very clearly (Fig. 10·10). So long as conditions are suitable, the birds will continue to occupy an area, though they thrive best in optimum habitat.

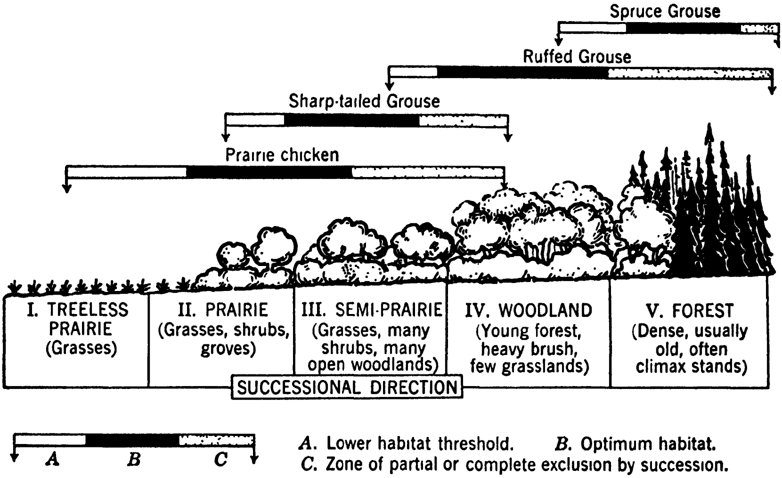
Spruce Grouse
Ruffed Grouse
Sharp-tailed Grouse
Prairie chicken
I. TREELESS PRAIRIE (Grasses)
II. PRAIRIE (Grasses, shrubs, groves)
III. SEMI-PRAIRIE (Grasses, many shrubs, many open woodlands)
IV. WOODLAND (Young forest, heavy brush, few grasslands)
V. FOREST (Dense, usually old, often climax stands)
SUCCESSIONAL DIRECTION
A
B
C
A. Lower habitat threshold.
B. Optimum habitat.
C. Zone of partial or complete exclusion by succession.

Fig. 10·10. *The overlapping requirements of the several Wisconsin Grouse illustrate the succession of species with change of vegetation in accord with ecological succession.* (*After Wallace B. Grange,* Wisconsin Grouse Problems, *p. 238. Madison, Wis.: Wisconsin Conservation Department, 1949.*)

In the course of human occupation of the land, changes usually mean *retrogression* on the ecological scale, such as are caused by the cutting of timber or plowing of the prairie. But succession itself advances the habitat. The most drastic bird upsets occur in the "down-grading" phase, but the longer-lived ones usually occur with succession advance. American birds well known for their tolerance of changed conditions include the Crow, Song Sparrow, Robin, Chipping Sparrow, Yellow Warbler, House Finch, Bob-white, and

Blue Jay. Those well known for their intolerance include the Raven, Kirtland Warbler, Ivory-billed Woodpecker, Pileated Woodpecker, and Spruce Grouse.

The spectacular success of the European House Sparrow and Starling in America illustrates the substituting ability of a species (Fig. 10·11). Just what their ecological adjustments were under native conditions is not clear, for both have been closely associated with man's artificial environment during ornithological history. Both perhaps nested in holes and crevices or perhaps occasionally built a nest in trees. House Sparrows in the South, for example, build their nests in trees far oftener than those in the North and also use buildings less often. They use palms freely. Perhaps reactions to air temperature account for their use of more exposed sites for nesting in the South. Table 10·2. shows some substitutions by birds of man-made structures for natural ones.

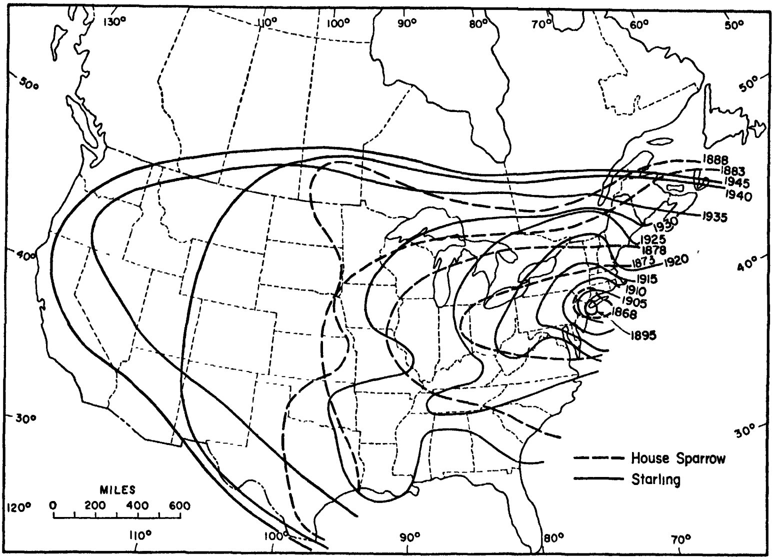

Fig. 10·11. *The House Sparrow spread faster in America following its importation than did the Starling. (Adapted from Leonard W. Wing, "The Spread of the Starling and English Sparrow,"* Auk, *60(1943):76.)*

Bird students generally assume that birds of the brush are more tolerant than others. So many common birds of the garden and farm have increased in abundance since settlement that this appears logical,

Table 10•2

Substitution of Man-Made Structures for Natural Ones.

Species	Original Site of Nest	Substitute
Wood Duck	Tree cavities, holes	Nest boxes
American Sparrow Falcon	Tree cavities, holes	Nest boxes
Screech Owl	Tree cavities, holes	Nest boxes
Purple Martin	Tree holes	Nest boxes
Barn Swallow	Caves, ledges	Buildings
Cliff Swallow	Cliffs	Walls, bridges
Tree Swallow	Tree holes	Nest boxes
Violet Green Swallow	Tree holes	Nest boxes
Eastern Phoebe	Cliffs, caves	Eaves, rafters, bridges
Chimney Swift	Hollow trees	Chimneys
American Robin	Trees	Buildings, bridges
Crested Flycatcher	Tree holes	Nest boxes
Osprey	Trees	Platforms
House Wren	Tree holes	Nest boxes

though it may not necessarily be so. Birds of earlier ecological stages have increased because more of this habitat is available. But wherever other habitat has developed, bird life has increased to fill it. The Horned Lark of the prairie has expanded its range, even in forest regions, wherever grass has replaced other vegetation. The Blue Jay of the forest has spread out into the plains where streamside ribbons and farmyard groves of timber provide the needed habitat. Adaptability to changed conditions in historic times seems to reflect tolerance for varying degrees of habitat suitability and a somewhat elastic capacity within the limits imposed by instinct.

RANGE

Size of Range. The size of range occupied by a species seems determined by a great many conditions of the bird and environment that together form the *range complex.* Chief among those of the bird are its instinctive habitat requirements, habitat tolerance, and adjustment to climate. Those of environment include vegetation, climate, and topography, as well as many others. But the actual determinant within the complex may be rather restricted. Small things within an area often determine use made of the habitat by birds or their survival beyond the general pattern. Limb density just below the forest crown, for example, is a critical factor limiting its use by Least Flycatchers; few Flycatchers used habitat having less than about 30 per cent openness (Breckenridge, 1956). Within broad areas of single vegetation type, niches for certain species may be small and limited to catastrophic areas in the forest, such as blowdowns, fire burns, eroded spots, or landslides.

The wide-ranging Osprey occurs throughout the world, and its range may be measured by continents. No other nonoceanic bird (except possibly the Barn Owl) touches practically all lands of the earth. In the case of oceanic birds, the great uniformity of oceanic environments provides the space for great ranges. Yet oceanic species may be confined to single ocean areas or zones of latitude.

The complex character of land environment operates against a single species spreading over much of the world while maintaining its species identity. The Raven of the Holarctic has done so with notable success. The Horned Owl of the New World ranges from the Arctic to the tip of South America, the greatest range among wholly New World species. It illustrates what often happens in wide-ranging land birds—they tend to subdivide.

Restricted ranges characterize many island birds and sometimes continental ones also. The Kirtland Warbler, for example, occupies but a few thousand square miles of breeding range in Michigan and the Golden-checked Warbler no more in the Edwards Plateau of Texas. Even more restricted is the range of the Cape Sable Seaside Sparrow, which inhabits only about two thousand acres of coastal prairie at Cape Sable, Florida (but it may be only an isolated pocket of birds belonging to a wider-ranging species). Other examples are the Ross Goose, Labrador Duck, Whooping Crane, Bristle-thighed Curlew, and Bachman Warbler. They may be *relict species* that survive where competition is least severe, as on islands or on continents by becoming more and more specialized. A relict species is one whose numbers or range or both have undergone drastic reduction (Amadon, 1953).

Continuity of Range. Generally speaking, the over-all range of birds forms a continuous one with but scattered pockets beyond the main limits. This is true especially perhaps of expanding ranges and those of more recent invaders to a land mass. The Mockingbird of southern United States occupies a continuous range broken only by local variations in its preferred habitat. But as mentioned elsewhere, the range of most birds consists of occupied habitat in a matrix of unused space. The Magpie of the West has spread eastward, but not by leap-frogging over suitable habitat—nor have the Horned Lark, Song Sparrow, Black-capped Chickadee, or a host of others whose ranges have increased.

Discontinuous Range. It is often easier to illustrate discontinuity of range than continuity, for the gap between calls attention to colonies of birds distant from the main body. Just as continuous range may mark an expanding or static species, discontinuous range seems often to be the mark of a species whose range has shrunk or shifted, sometimes the result of a major geological event. The most recent of these, the Ice Age, has left its mark on many discontinuous ranges. The Red-breasted Nuthatch, for example, occupies much of the northern coniferous forest of North America. Two remnants live in the Old World, one atop the mountains of Corsica in the Mediterranean Sea and a second in Eastern Siberia and China. All are distant from each other. Since these birds have low flight powers, we can justifiably conclude that they are remnants living in separated parts of a former wide range, rather than in advance pockets of recent expansion. The probable explanation lies in a formerly widespread Holarctic distribution broken up by events of glacial times. More recent geological events may have been involved also.

Influence of Mobility on Range Occupation. The very great power of flight does not relieve birds from the limiting actions of distance—it only sets the limits farther away. Nesting, resting, feeding, and escape cover must be at hand for a bird of high as well as of low flight powers. A Mockingbird requires trees in open grass areas, all within a few yards or rods, but the habitat needs of a Golden Eagle may be separated by miles. A desert bird requiring water daily would be limited by its travel distance, as would also any bird in finding its daily food. But distinguishing flight limits as a control from actual instinctive aversion makes any interpretation difficult.

An ingenious calculator concluded that because the Chimney Swift seldom perches from early morning to late at night (in good weather at least), a banded one known to have lived at least 9 years flew 1,350,000 miles in the nine years of living and nine trips to South America and back to the United States. For each year of life beyond nine, 150,000 more miles would be added. For a bird that remains aloft for hours at a time, the interspersed nature of its living needs might not be so important a control as for a bird of less flight range. In any event, makers of precision equipment might well envy the lasting qualities of the bird mechanism.

Distribution of Closely Related Species. The closer the relationship of species, the closer ecologically and geographically should we expect to find their ranges, but historical events may alter this relationship.

The ranges of *allopatric* species (*geographic complements*) may be expected to form a continuous range. One species declines in numbers as it is replaced by the other and the combined density in the

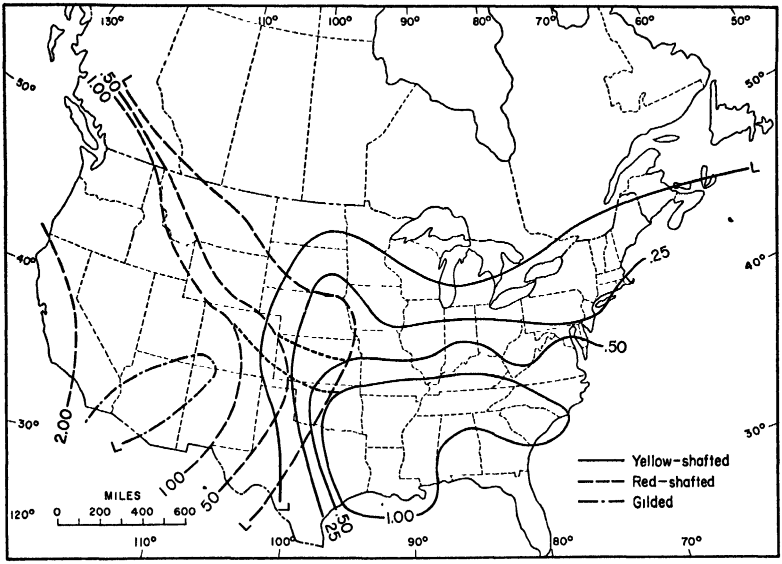

Fig. 10·12. *The winter ranges of the allopatric Flickers illustrate geographic complementing, the one species declining in numbers as the other increases. The figures are the average birds-per-hour of the Christmas Censuses, 1900–1939. A dotted connection between the respective isopleth line indicates combined abundance.*

zone of overlap remains equivalent to the separate abundance in the respective areas, as shown by winter data of the Red-shafted and Yellow-shafted Flicker (Fig. 10·12). The Mallard and Black Ducks show this also (Fig. 10·13).

The ranges of *sympatric* species, like the Hairy and Downy Woodpeckers, overlap rather generally, but the larger member of the pair tends to have the more northerly distribution, at least in winter (Fig. 10·14). Exceptions may occur, however, as in the Cooper and Sharp-shinned Hawks. The smaller Sharp-shinned nests farther north, but the larger Cooper Hawk tends to winter farther north in greater numbers and biomass.

Origin of North American Bird Life. Though the past history of bird life does not furnish the evidence for detailed tracing of origin, development, and spread (as has been done with some larger mammals), a general pattern of origin for North American families has been proposed (Mayr, 1946). The largest contributors of species are North America itself and the Old World (Fig. 10·15).

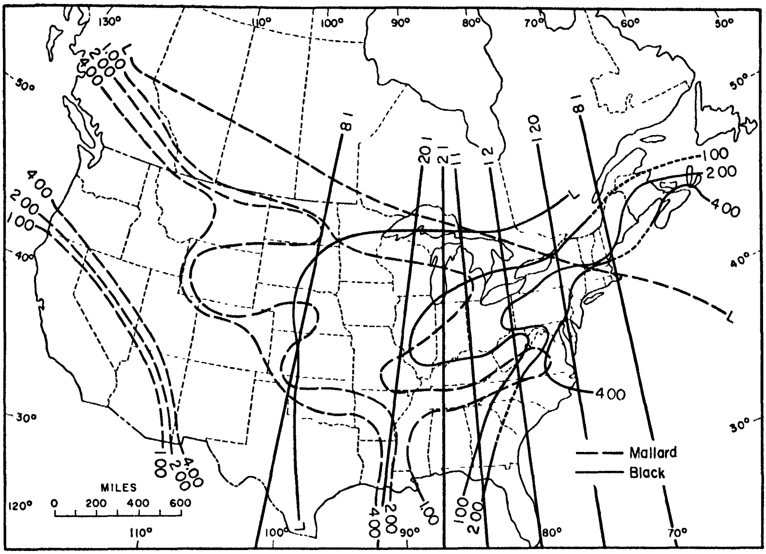

Fig. 10•13. *The ratio lines indicate change in proportions of Mallard and Black Ducks as reported in Christmas Censuses. The Mallard outnumbers the Black Duck in the West. (From Leonard W. Wing, "Relative Distribution of Mallard and Black Duck in Winter,"* Auk, *60(1943): 439, and Christmas Census data, 1900–1939.)*

North America shares with South America a number of families that have not spread into the Old World (except incidentally on the Siberian shore) though they are expanding their ranges now. Examples of these are the New World Warblers (Parulidae), Vireos (Vireonidae), Flycatchers (Tyrannidae), Tanagers (Thraupidae), Hummingbirds (Trochilidae), and Icterids (Icteridae). But some seemingly vigorous Old World birds (e.g. Hoopoes, Pittas, Rollers, Sunbirds) have not reached the New World, at least so far as living birds of today are concerned.

The nonoceanic birds of North America represent several areas of origin which have been listed as the Pantropical, Old World, North American, and South American, with perhaps a Pan-American one (Mayr, 1946).

Examples of each follow:

PANTROPICAL

Anhingidae
Rhynchopidae
Psittacidae
Trogonidae

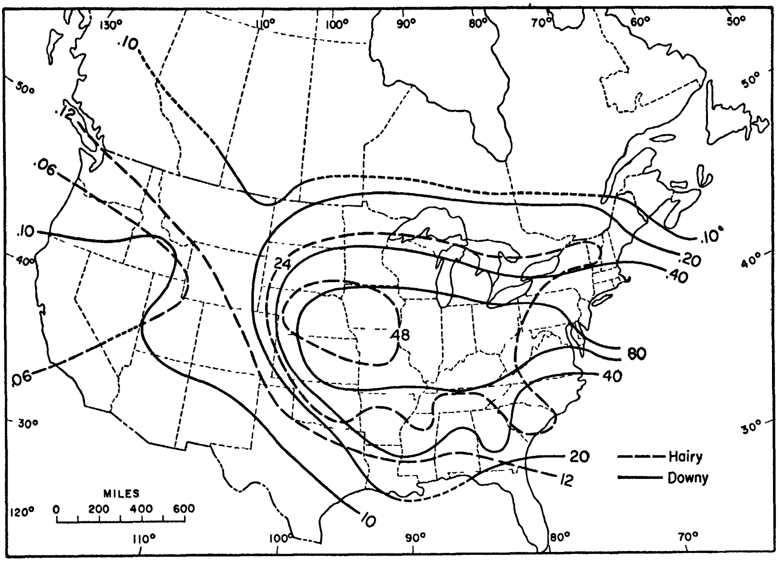

Fig. 10 • 14. *The winter ranges of sympatric Hairy and Downy Woodpeckers show no geographic complementing. The numbers shown for the Plains Country reflect concentration of birds in river bottoms. (Christmas Census data, 1900–1939.)*

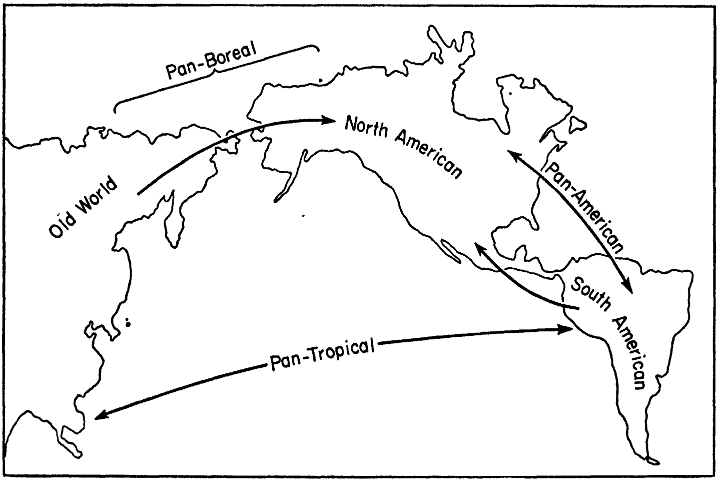

Fig. 10 • 15. *Diagram of the faunal elements of North America. (After Ernst Mayr, "History of the North American Bird Fauna,"* Wilson Bulletin, *58(1946):3–41.)*

Old World

Gruidae
Columbidae
Cuculidae
Strigidae
Tytonidae
Corvidae
Alcedinidae
Paridae
Sittidae
Motocillidae
Alaudidae
Hirundinidae
Certhiidae
Turdidae
Sylviidae
Laniidae

North American

Cathartidae
Tetraonidae
Meleagrididae
Cinclidae
Troglodytidae
Bombycillidae
Parulidae

South American

Tinamidae
Anhimidae
Ramphastidae
Formicariidae
Cotingidae
Pipridae
Coerebidae

Pan American

Cracidae
Trochilidae
Tyrannidae
Thraupidae
Icteridae

Enough is known of families (or their groups have diverged enough in some cases) that origin of subgroups appears determinable. In the Finch family (Fringillidae), the subfamily Carduelinae appears to have immigrated from the Old World, Richmondeninae came from South America, and Emberizinae developed in North America. The Kinglets of the family Sylviidae came to America from the Old World, but the Gnatcatchers arose locally. The Quails (Odontophorinae) arose in America, but the rest of the Phasianidae, as well as the family itself, arose in the Old World.

As would be expected, the Old World element appears most frequently in the North American boreal zone (geographically nearest to the Old World land mass) and the South American element in the austral zone. The North American element appears most frequently in the more isolated middle latitude and especially in the interior prairie region (Table 10·3). The interior prairie region seems to have had few floral connections with comparable vegetation zones. (The marine influence on climate in the North Pacific would have precluded a connection northwestward, and both dryness and the wet tropics would have done likewise southward.)

Table 10·3

Analysis by Geographic Origin of the Breeding Passerine Species of Several North American Areas

District	Percentage of South American Origin	Percentage of North American Origin	Percentage of Old World Origin
Yakutat Bay (Southeast Alaska)......	3	39	58
Oregon	14	47	39
Nipissing Area (Southern Ontario)...	13	57	30
New Jersey	14	63	23
Florida	20	59	21
Sonora, Mexico	27	52	21

Source: Ernst Mayr, "History of the North American Bird Fauna," *Wilson Bulletin*, 58(1946):3–41.

Within the North American continent, western birds drift and wander eastward far more often and more successfully than the converse. The general westerly winds of mid-latitudes may be involved. Representatives of Old World families have penetrated the American Tropics. It may well be that birds of cooler regions become adapted more easily to warm climates than the opposite. But because the climate occurring at the Bering land bridge would govern any transfer of bird life, northern birds would always have the advantage. The past climate of the North Polar region has varied (Berry, 1930). Only by progressive adaptation and spread or only when climatic belts move bodily northward would southern birds be in a favorable position to cross. An arid zone across northern Mexico and southwestern United States has probably acted as a barrier from very ancient times, as has also a more humid zone nearer the Alaska land bridge.

The invasion route across the Alaska land bridge is on the western side of North America. Like all immigrants, the new arrivals settled down in the nearest suitable land. Their descendants have slowly spread eastward to occupy ranges variously eastward from the western side where first their ancestors landed. There seems to be no reason to assume that the process has ended, either for those having already gone across the land bridge or for others that might do so. The path of spread between the Old and New Worlds hence accounts for the greater similarity between the bird life of western Europe and western North America than between western Europe and eastern North America, several thousand miles closer. The Nutcrackers, Waxwings (Bohemian), Magpies, Dippers, and many others of western North America are found also on the Eurasian continent.

SUGGESTED READING

*Armstrong, Edward A., *Bird Display and Behavior.* London: Lindsay Drummond, Ltd., 1947.

*Armstrong, Edward A., *Bird Life.* New York: Oxford University Press, 1950.

Dice, Lee R., *Biotic Provinces of North America.* Ann Arbor, Mich.: University of Michigan Press, 1943.

*Griscom, Ludlow, *Modern Bird Study.* Cambridge, Mass.: Harvard University Press, 1945.

Hesse, Richard, W. C. Allee, and Karl P. Schmidt, *Ecological Animal Geography.* New York: John Wiley & Sons, Inc., 1951.

Lack, David, "Ecological Aspects of Species-Formation in Passerine Birds," *Ibis,* 86(1944):260–286.

Mayr, Ernst, "History of the North American Bird Fauna," *Wilson Bulletin,* 58(1946):3–41.

Miller, Alden H., "Habitat Selection Among Higher Vertebrates and Its Relation to Intraspecies Variation," *American Naturalist,* 76(1942):25–35.

11

Ecological Relations of Birds

While there are many definitions of ecology, it seems most satisfactory still to return to the early one that *ecology is the study of the relation of an organism to its environment.* Hence, most activities of living birds come under the term *ecological relations* in the broadest interpretation of the word. It seems best at this point, however, to consider only a few of these relationships.

The success or failure of an individual bird (and the species to which it belongs) lies in the reactions of its body mechanism—physical, physiological, and otherwise—to the biological hammering and cushioning of the environment. This goes on all day long and all night long; it continues in summer and in winter. It goes on during the fleeting instant when a bird passes across the observer's field of vision, just as it does during the rest of the bird's life, though unseen by an ornithologist as the bird lives out its life in the bush, the tree, the marsh, the shore. Some of this matters little to the bird, some of it matters greatly. But to students of nature and its science, it tells a story; that story we call *ecology.*

THE ENERGY BASE

Biological Energy. The source of all energy for the bird comes from the sun, and all birds obtain this energy second hand from the plants or even further removed if taken from other animal life (see Chapter 23). Plants form the biological portal through which energy enters the bird world. Plants, which are about 18 per cent efficient in using solar energy, by photosynthesis transfer energy from the sun to organic compounds through appropriate chemical action involving primarily carbon dioxide of the air, water of the soil, and soil nutrients.

The biological energy potential is highest in equatorial regions where the greatest amount of solar energy reaches the earth. In mid-latitudes, the energy usable in photosynthesis amounts to a flow of about 150 horsepower per acre. The most important earth influence determining how great an expression the biological energy potential reaches is moisture, for only when they have sufficient moisture will plants utilize to their fullest the energy of the sun. The desert coast of South America lies under the full tropical sun, for example, but plants there do not extract from the sun the great quantities of biological energy entrapped within a Michigan woodland or an Oregon forest. With about the same solar exposure, the coast of South Carolina has a greater total of plant and animal life than that of southern California. The reason, as stated above, is that areas with a goodly water supply extract more biological energy than dry ones.

The entrapment of biological energy may vary also with other environmental factors. Along a coast where cold winds blow in from the sea, the low temperature does not permit plants to extract energy as they would at the same latitude with warmer air temperatures. The presence of fog and cloud screens out the sun's rays. A water habitat may produce more life than a land habitat because of water availability, but local conditions of turbidity, temperature, acidity, or alkalinity may interfere. Increased altitude means greater reception of sun's rays because of less atmospheric screening, but the cooler temperatures of higher altitudes offset these gains.

Biological Energy Competition. It is axiomatic in thermodynamics that when two mechanisms compete for the same source of energy, the more efficient of the two prospers at the expense of the less efficient one. We should expect in nature that the more efficient organism has an advantage over a less efficient one. By that token, the environmental complex native to an area appears to be the most efficiently adapted for use of the biological energy of that area. In terms of ecology, it means that the climax is the most efficient stage. The principle assumes, which is a point of weakness, that a complete array of life has had access to the area and the survivors are the current victors in the struggle for use of the area's biological energy resources.

SUCCESSION AND HABITAT

Ecological Succession. An area undisturbed and in adjustment with the climate is termed a *climax.* Adjustment to the climate means that plant and animal life live essentially in a state of equilibrium, the entire complex renewing itself as before. But when such an area is disturbed, it returns to the climax through successive recognizable and predictable stages. This process is *ecological succession*, each step a stage, and all steps together constitute a *sere*. Succession in water habitats forms a *hydrosere*, that of land a *xerosere*. (Weaver and Clements, 1938). An example of a hydrosere (freshwater) with some representative birds may be listed as:

Submerged Stage
  Water less than 20 feet deep, Diving Ducks, Grebes, Coot
Floating Stage
  Water 6 to 8 feet deep, Dabbling Ducks, Gallinules, Coot
Reed-Swamp Stage
  Water 1 to 4 feet deep, Dabbling Ducks, Gallinules, Rails, Red-winged Blackbirds
Sedge-Meadow Stage
  Water below but near surface (except in flood), Meadowlark, Savannah Sparrow, Bittern
Grass Stage (in grassland region), Meadowlark, Lark Bunting
    or
Woodland Stage (in forest region), Wood Thrush, Blue Jay.

A xerosere (dry land) example beginning with bare ground and some representative birds may be listed as:

Crustose-Lichen Stage, no characteristic birds
Foliose-Lichen Stage, no characteristic birds
Moss Stage, no characteristic birds
Herbaceous Stage, Vesper Sparrow, Meadowlark, Horned Lark
Shrub Stage, Cardinal, Yellow Warbler, Chat
Climax Forest, Acadian Flycatcher, Scarlet Tanager

The speed of succession varies with regions. In low latitudes it is rapid, often passing from the bare ground to the forest stage in 10 to 20 years. But near the *Limit of Trees* in the Arctic, the time necessary for comparable progress may be ten times that of mid-latitudes. A schedule in Tennessee perhaps would be as follows (Wing, 1940):

Bare ground—first year
Weeds—first to third year
Forbes—second to fifth year
Grass—fourth to sixth year
Briar—fifth to seventh year
Brush—sixth to twelfth year
Forest—ninth to eighteenth year

Habitat. The environmental complex that satisfies the bird is the *habitat*, though we commonly think of habitat only as the vegetation type in which a bird lives. The term habitat in the animal world, it

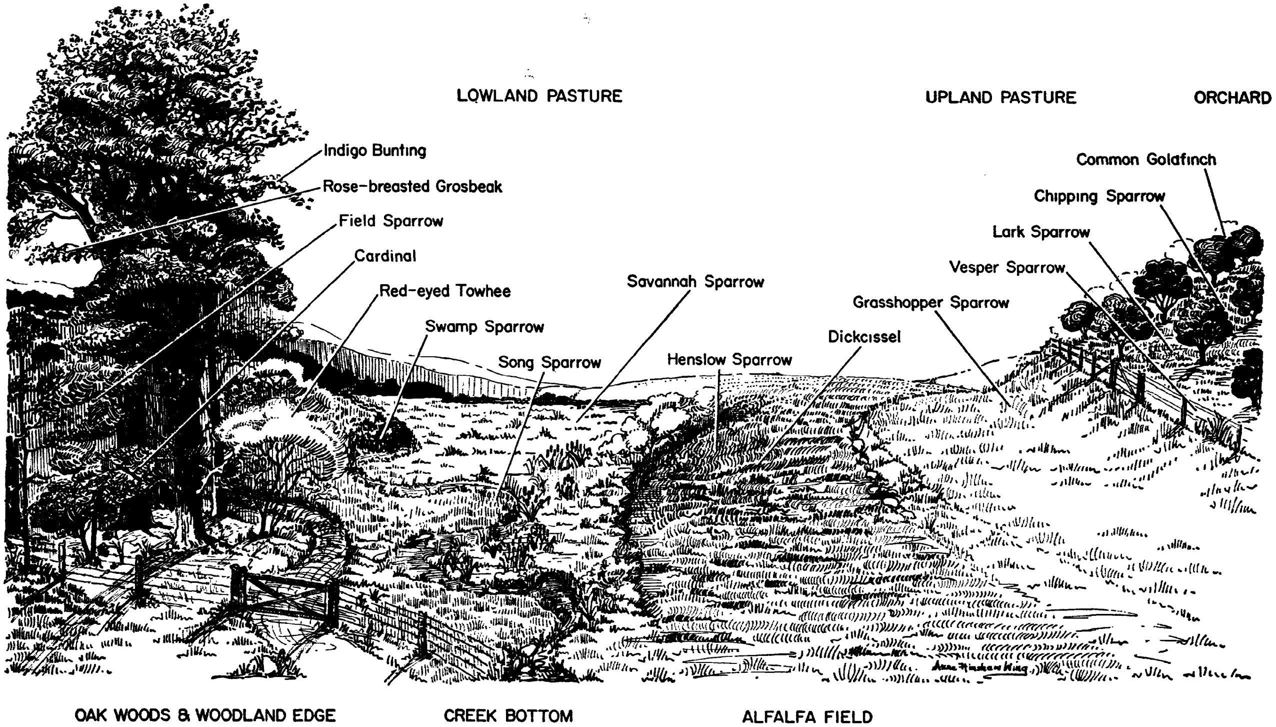

Fig. 11·1. *Idealized cross section of a farm area in Washtenaw County, Michigan, to show ecological segregation among the native Finches (Fringillidae) during the breeding season. (Prepared by Anne Hinshaw Wing.)*

should be noted, has much the same meaning as *site* to the plant in the plant world.

Within the environment exist combinations of habitat factors that provide the life-opportunity for each species. Each combination of factors forms a *niche* occupied by a species. In the Book Cliffs of Utah, three species of birds live permanently in the pigmy conifer forest but avoid competition by differences in food habits and nest selection (Hardy, 1945). Five semipermanent species avoid this competition by using nest cavities of different sizes, by nocturnal habits, by different feeding habits, and by different spatial habits. In the competition of life, it seems axiomatic that no two species of birds can occupy the same niche at the same time any more than two objects can occupy the same space at the same time.

The birds of any major habitat have developed differences in niche requirements, partly from behavior patterns, that avoid interspecies competition and strife (Fig. 11·1). The New World Warblers (Parulidae) illustrate this very well in their selection of territories. Twelve species living together in the mixed conifer and deciduous forest region of eastern New York, an area severely disturbed by man, have separate niches determined in part by differences in the vegetation used and in choice of nesting site (Table 11·1). Similar variations in choice of vegetation occur in other groups of related birds or birds of the same general environment.

Table 11 · 1

Nest and vegetation selection by Warblers

Species	Vegetation Selected	Nest Site
Black and White	Tree trunk	Ground
Nashville	Sunlit open conifer	Ground
Magnolia	Low level conifer	Conifer branches
Black-throated Blue	Shaded shrub	Shaded brush
Black-throated Green	Middle level conifer	Branches
Blackburnian	Top level conifer	Branches
Chestnut-sided	Sunlit shrubs	Shrubs
Ovenbird	Dry shaded ground	Dry ground
Louisiana Water-thrush	Wet shaded ground	Moist ground
Yellowthroat	Wet sunlit ground	Low vegetation
Canada	Moist shaded ground	Moist ground
Redstart	Second growth hardwoods	Low forks

Source: In part after S. Charles Kendeigh, "Community Selection by Birds on the Helderberg Plateau of New York," *Auk,* 62(1945):418–436.

Although the *macroclimate* of a region may remain much the same, birds may respond to differences of *microclimate*, a matter of which we know little. Other environmental factors are subject to variations in choice. Some birds prefer the low light intensities of shade and others the high light intensities of tree tops or the open. Even perches play a part in the choice of niche.

Major Habitats. For purposes of simplicity, it is customary to list birds by their major habitats. The ten broad designations most commonly used are forest, brush, grassland, desert, marsh, lake, stream, shore, ocean, and bare ground. But each of the ten may be subdivided into a large number of habitats. The forest for example, may be divided readily into conifer, deciduous, and broadleaf evergreen forests. The latter may be divided again into tropical, subtropical, and mid-latitude broadleaf forests. The grassland (open range) may be prairie, steppe, savanna, meadow, dune, and sometimes moor, tundra, or mountain tundra. Deserts may be of many kinds, such as chaparral, thorn thicket, cactus, shrub forest, sagebrush, salt flats, or "desert waste."

The ocean covers 72 per cent of the earth's surface yet it contains but a small fraction of the bird life. Even the birds able to live pelagic lives, like the Shearwaters, Petrels, and Albatrosses, must return to land for nesting. So far as marine bird life is concerned, its greatest abundance occurs where the largest quantity of available, supporting marine organisms are found (Murphy, 1936).

The largest habitat in North America and perhaps Eurasia is the open range habitat, which embraces tundra, grassland, and much of the desert; it contains about 40 per cent of the land area in North America. The second largest is the conifer forest habitat, with 30 per cent in North America; and the third is the deciduous forest habitat, with about 15 per cent. For the world as a whole, the major habitats from the natural vegetation standpoint may be estimated as in Table 11·2.

Table 11·2

Estimated Thousands of Square Miles of Major Bird Habitats in the World

Habitat	Area	Habitat	Area
Forest	21,500	Lake	550
Grassland	12,500	Stream	800
Desert	17,000	Shore	1,000
Marsh	2,500	Ocean	138,000
Other	6,500		

Vegetation Zones. The bird student in the field may not often find any named systems described in Chapter 10 useful except perhaps as general or broad geographic designations—for which purpose political, geographic, or climatic regions may be just as suitable and sometimes more so. But for major comparisons, biogeographical designations may serve a very useful purpose. It is clear that no system yet devised will serve adequately the needs of bird students, though such terms as *Canadian* or *Coniferous Forest* convey a definite meaning. If the nature of the systems is understood, however, one is about as useful as another for bird work.

In the field, vegetation zones usually will be the most useful classification for bird work. Such zones are really *cover types*, the scale of zonation being governed by fineness of the study. Vegetation zones suggested for the northern intermountain region (Daubenmire, 1946) serve as an example of altitudinal zones useful in bird work:

- Mountain Tundra
  - Sedge-grass zone
- Conifer Forest
  - Spruce-fir zone
  - Arborvitae-hemlock zone
  - Douglas fir zone
  - Ponderosa pine zone
  - Juniper-piñon zone
- Prairie
  - Fescue-wheatgrass zone
  - Wheatgrass-bluegrass zone
  - Needle-grass–gramma grass zone
- Semidesert and Desert
  - Sagebrush-grass zone

Table 11·3
Vegetation Zones of Mexico

	Per Cent of Area	Square Miles of Area	Yearly Rainfall in Inches
TEMPERATE ZONE			
Boreal forest	0.5	3,800	30–74
Pine-Oak forest	25.8	195,600	18–70
Chaparral	1.2	9,100	14–30
Mesquite-grassland	21.6	163,700	9–36
Desert	23.1	175,100	2–15
TROPICAL ZONE			
Cloud forest	0.5	3,800	70–200
Rain forest	7.3	55,300	60–200
Tropical evergreen forest	5.5	41,700	36–112
Savannah	0.9	6,800	34–100
Tropical deciduous forest	9.1	69,000	24–60
Thorn forest	3.2	24,300	16–34
Arid tropical scrub	1.3	9,800	12–28
Total	100.0	758,000	(Average 38.6)

Source: A. Starker Leopold, "Vegetation Zones of Mexico," *Ecology*, 31(1950): 507–518.

Vegetation zones may parallel climatic conditions, and the major vegetation zones of Mexico illustrate this rather well (Table 11·3).

Life zones and biomes (Chapter 10) have the fundamental weakness of using the climax as their bases. Since man has interjected himself into the landscape, so many areas have been so completely subjugated to his action that climax classifications may have only academic or historical significance. Vegetation zones or types that indicate by their names the principal character of the type are useful. Thus, second-growth hickory, sagebrush-bunchgrass, and thorn forest mean something definite. Though not often to be recommended, terminology based upon the bird life of an area might be used if one so chooses. A *Hermit Thrush zone*, *Meadowlark zone*, or *Yellowthroat zone* would mean something to a bird student, though probably not much to others.

COVER AND COMMUNITY

Cover Type. The preceding sections have suggested the use of classifications that indicate the land as it exists today or that are based upon the land as it now appears. In a sense, these are all cover types, though we usually use the term for small areas, generally for local vegetational types. A farm or a forest may have a dozen cover types within its borders. A common method of indicating forest cover types, for example, is by means of tree species, size, and spacing. A cover map forms an excellent base on which to indicate bird territories, movements, nests, or other field data. Cover types for a general midwestern American farm might include some of the several given below:

Cover Types Common to American Midwestern Farms

Fallow fields
Weed fields
Ragweed
Hay field
Orchards
Abandoned fields
Beech woods
Oak woods
Hickory woods
Brush fence rows
Grass fence rows
Seeded pastures
Grass pastures
Marsh
Brush
Brush draws
Swamp hardwoods
Brush pasture

Interspersion of Cover. In a sense, birds require a variation in cover just as do other organisms, which in the breeding season usually involves a mixture of cover types or species. Cover formed of a single plant species usually supports far fewer birds than a mixture of several species; a single species cover type of all age and size classes has greater attraction than a uniform one. The mixing of plant species (*interspersion*) directly affects bird numbers and success. In addition to this factor, the various requirements of the bird must be within reach as governed by its *cruising distance.*

The Mockingbird of southern gardens and lawns illustrates the need for interspersed cover. Its needs include (1) grass areas such as lawns on which to hunt food, (2) brush in which to nest, rest, hide, and feed, and (3) trees from which to sing and in which to roost. A 150-acre area in which these needs were proportionately spaced could have a pair to the acre and perhaps even more. But if all the trees were concentrated in an 8-acre woodlot, all the brush in a 30-acre field, and the grass in a pasture, the 150-acre tract would have no Mockingbirds except for a few where the woodlot, brush, and pasture meet.

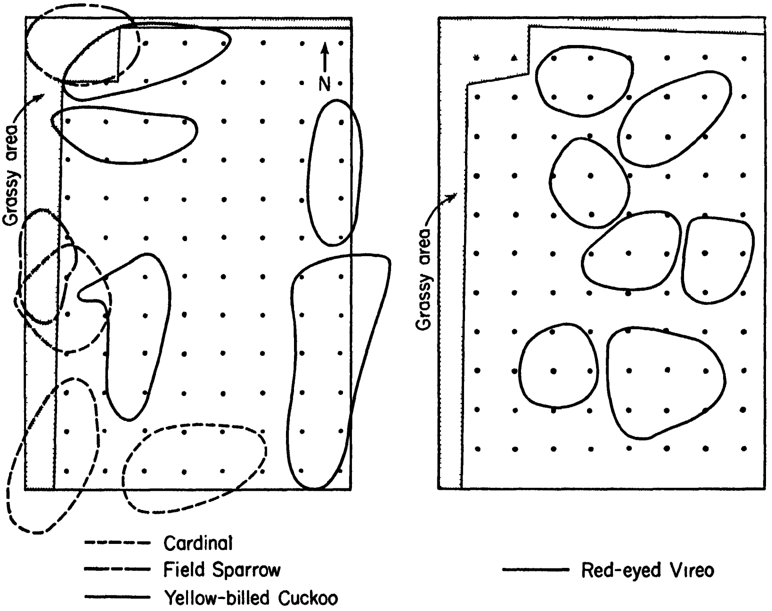

Fig. 11·2. Left. *Territories of the Cardinal, Field Sparrow, and Yellow-billed Cuckoo, all forest edge birds.* Right. *Territories of the Red-eyed Vireo, a forest interior bird. The dots indicate a 50-meter grid of a 56-acre woods near Urbana, Illinois.* (*After Verna R. Johnston, "Breeding Birds of the Forest Edge in Illinois,"* Condor, *49(1947):45–53.*)

The advantages of access to more than one kind of cover along the boundary where cover types meet show in the greater abundance of birds there. Some species will be found only in the forest interior, some in the interior and border, and some only along the border (Fig. 11·2), but they are usually most numerous along the edge. From this has developed the concept of edge effect, an edge being the meeting of two plant types. Edges exist in open fields where grass gives way to weeds, in lakes where the shallow-water *Scirpus* gives way to water lilies, and in the forest where pines give way to spruces. (Ecologists, be it noted, sometimes call an edge by the term *ecotone.*)

Cover Volume. Forests tend to have stratification of bird life, so that several species may occupy the same ground surface but at different levels. The *volume* of vegetation available to birds thus plays an important role in bird numbers. Ornithologists have still to determine the factors governing abundance of species and numbers in relation to volume. That it is not proportionate seems certain. One of the reasons for this rests in the fact that the energy reception by the forest concentrates in the canopy where light is greatest, just as it does in a brush patch. A forest of trees 100 feet high, especially the nonconifers, has about the same crown exposure to catch sunlight as a forest of 50-foot trees. The difference in entrapment of biological energy lies largely in the space between the crown and the ground. In some forests this may be rather uniformly filled with shrubs and small trees, but in others there is little undergrowth. The light from the sun that filters down is but a part of that hitting the forest roof.

Shelter and Roosts. The shelter needs of most birds may seem to need little discussion, they are so abundant; yet exact knowledge of even general shelter needs is far from adequate. As most shelter requirements will be covered in appropriate places, it may be unnecessary to elaborate greatly upon the subject in this section. Shelter itself sometimes differs in connotation from *escape cover* in that a bird uses shelter for protection from the elements and escape cover for protection against enemies. As has been indicated already, both are definite physical identities that must satisfy the instinctive make-up of the bird.

Night roosting occurs in characteristic situations, all related to the bird's diurnal habits, but our knowledge of the subject is woefully deficient. Hole-nesting birds generally roost at night in holes, often the one used for nesting. Chickadees sometimes roost together, perhaps a whole flock in one hole if it is large enough. The Swallow habit of roosting among the reeds in marshes is well known. The Chimney Swift roosts in chimneys, sometimes by the thousands during migration. During the summer in parts of the West, Cliff Swallows spend the night in their nest-pots fastened to cliffs. In winter these same nest-pots may be used by Rosy Finches from the high country (Shaw, 1936).

The average Passerine bird roosts in brush or in trees, usually hidden in the foliage or twigs. Most prefer thick branches or even vines when available. But some birds, such as Nighthawks, perch on the main branches (sometimes in flocks made up largely of males during the summer). Owls often roost on a branch, sometimes close to the trunk. Birds like the Song Sparrow settle down in brush or thick marsh vegetation. The White-throated Sparrows and others of brush and hedgerows perch in the brush for the night.

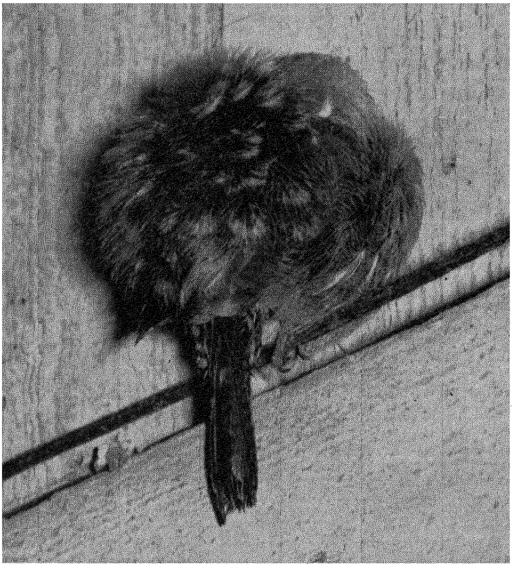

Fig. 11·3. *The night-roosting Bewick Wren fluffs up its plumage to form a ball of feathers.* (*Photograph by Laidlaw Williams.*)

Ground birds, even Passerines, may spend the night on the open ground or in clumps of grass. Savannah Sparrows may settle on the bare ground and Meadowlarks in the grass. The Valley Quail roosts in low, heavily foliaged trees. The hours on the roost reported in California varied from 8 hours, 18 minutes on July 5 to 13 hours, 33 minutes on November 26 and probably still more in December and January (Sumner, 1935). The Ruffed Grouse spends the night in thick, wind-resistant clumps such as conifers or grape tangles, usually close to the main trunk. (In cold weather when the snow is deep, they may burrow under the snow for the night.) Ptarmigan may burrow under the snow or roost in depressions in the snow. Prairie Chickens and Sharp-tailed Grouse may fly several miles to favored dry marshes or other sites for the night.

Most ducks and other waterbirds may spend the night in the open water, but some spend the night on shore. Shorebirds and many Gulls and Terns spend the night on the bars, beaches, and shore.

The roosting bird fluffs up its feathers, which increases the thickness of the insulating air blanket. A Bewick Wren pulls its head in and fluffs up like a ball, with only its tail extending beyond the smooth contour of the feathers (Fig. 11·3). Some birds turn the head back into the scapular and back feathers. This may protect the eyes, nostrils, and thinly covered face from cold in cold regions, but some birds of tropical and subtropical regions do likewise (*Buteo magnirostris* and the *Faisáno Real* of Mexico, for example). The bend of the wing may be lifted to cover part of the face.

Influence of Instinctive Needs. Animals have become adapted to their environment and have developed a set of instincts fitting them to their efficient use of the surroundings (Chapters 10 and 23). While this may not be the most efficient use theoretically possible, it seems to be as efficient as needed in the battle of life.

A bird that lives in the woods, like a Chickadee or a Nuthatch, does so because woods alone supply its instinctive needs for habitat. These birds have developed characteristic feeding habits, nesting habits, and behavior patterns adjusted to their way of life in the woods (Fig. 11·4). The duckling, even a newly hatched one, seeks the water because water satisfies one or more of its instinctive needs. In the same way, other birds seek their characteristic habitats because only these satisfy their instinctive needs. Those not wholly satisfying instinctive needs, either correctly or by acceptable substitutes, will be used only proportionately for the fulfillment of these needs. They are *marginal* habitats which but partially supply the needs of life.

Habit and tradition may play a part in the use of habitat, though their influence may be transitory only. The bird hatched and raised under one set of conditions may, when it shifts for itself, seek similar ones because of *imprinting*, though how much this controls the action of wild birds is problematical. A possible source of testing this factor lies in comparing the behavior of socially parasitic birds. Young Cowbirds hatched in nests of Warblers, for example, could reflect their early life and perhaps act differently in a measurable way from others raised in Fringillid nests. But there seems to be no clear evidence to indicate that this happens, though it might be a fruitful study.

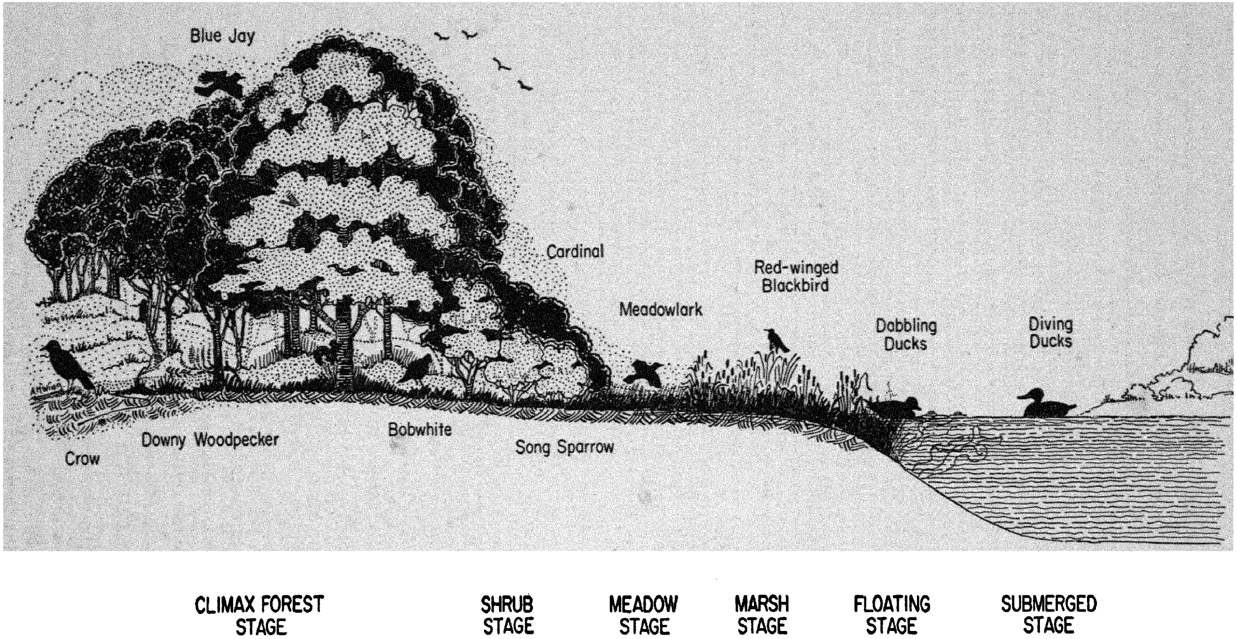

Fig. 11·4. *Each species of bird has its habitat choice. This diagram indicates the ecological change in a forest area from water habitat to forest habitat. Examples are given of birds found in each successive stage. (Prepared by Anne Hinshaw Wing.)*

Community Relationships. A *community* in the ecological sense consists of the organisms living together. It is hardly a "super organism" as enthusiastic ecologists have said but includes only such plant and animal life as live in the same delimited area. Birds depend upon vegetation and lower forms, and an interdependence of organisms thereupon occurs in varying degrees. Thus, the insect-eating birds depend upon the insects which depend upon the plants. But plants depend upon only relatively few of the insects, sometimes upon none, and few insects actually depend upon birds for life success. Yet the presence of part of the community of organisms necessitates presence of those that mutually hold each other in check. In the sense of "all or none," it can be said that interdependence may often be rather great.

As the breeding potential is so great, bird life necessitates destruction of the excess; it may be said truly that animals depend upon both their enemies and their competitors for life success. Often "dependence" is but a small thing, as when the warning note of a Blue Jay calls attention to a marauding cat. Yet along the Florida coast, ecologists report that the presence of organic fertilizers from bird colonies is essential for the rich aquatic plant and animal growth in adjacent waters that in turn support the colonies (Mills, 1944).

Carrying Capacity. It may seem facetious to remark that a bucket can carry no more water than it can hold were it not that this rather suggests the principle of *carrying capacity* as applied to birds. Every habitat has a limit as to how many birds may live there in safety. It may vary from zero in unsuitable habitat to the *saturation point* of the species in favored habitat. The saturation point is actually a function of the bird; it is the maximum density to which they will go by themselves. In a sense, it measures the willingness of birds to be squeezed into small areas or into high densities. Carrying capacity, on the other hand, is a function of the land. But it is measurable only by the birds that use it; it cannot be measured above the saturation point, for that is the limit set by the birds themselves.

Birds in the wild, being free agents, move about and occupy habitat of their own volition (discounting the fact that they may be under compulsion of instincts, such as that for reproduction). Birds already in a habitat may ignore newcomers or engage in conflict. Hence, carrying capacity is not the number that can be forced into an area but the number adjusted to the habitat and the toleration of others.

For ordinary purposes, the carrying capacity may be considered as the maximum number (maximum biomass probably would be better, page 256) that an area can support adequately during the most severe or poorest time of occupancy—the *pinch period.* For resident birds of middle and high latitudes, this usually is the winter. For low latitudes, however, it is usually the dry season. For desert birds, it would be the dry season or the winter. Carrying capacity thus is a function of the land. Good habitat with a favorable climate has high carrying capacity (according to species); poor habitat and habitat with seasonal extremes has low carrying capacity. The governing point is how well the habitat meets the needs of the species. The mobility of the birds, however, makes it possible for them in some instances to move in and occupy in great numbers during a short and favorable interval an area not otherwise wholly suitable. Some of the concentrations in the Arctic nesting grounds of many birds exemplify this. In a sense, it is shown also by all migratory birds. Concepts of carrying capacity would be adjusted accordingly.

SEASONAL INFLUENCES

Seasonal Change. Change of season forms the dominant characteristic of the middle latitudes where large human populations live. Therefore, this great feature of the environment very properly may be given the most earnest consideration. But in so doing, we must not fall into the error of thinking that seasons in the low latitudes change in the same way as they do farther north (or south). The temperature in equatorial regions may vary more during the day than does its average for the months of the year. The rainfall may be evenly distributed or it may vary greatly from a marked dry period to a pronounced wet one.

The variation in seasons rests on the fact that in its yearly pathway around the sun, the axis of the earth itself is tipped 23½° from a perpendicular with the plane of its orbit. Because the axis remains parallel to its own position at all times of the year, one pole will point toward the sun part of the time and away part of the time; meanwhile, conditions at the other pole will be just the opposite. The daily lengthening of sunshine and the angle of the sun will vary at all places throughout the year. Beyond the Arctic and Antarctic Circles (23½° in latitude from the respective poles) it will vary throughout the year from 24 hours in summer to none in winter. The vertical rays will move from 23½° on one side of the Equator to 23½° on the other (Tropics of Cancer and Capricorn). This shift of 23½° in the sun's apparent position shifts the climatic belts—even in the equatorial lands, where rainy and dry seasons may result. The cause thus is the same for winter-summer seasons in the high latitudes and for wet-dry seasons in low ones. Upon these seasonal changes rests a whole series of repercussions in the bird world.

Phenology. Just as succession progresses in an orderly manner over the years, the change of seasons progresses systematically. To the progress of seasonal phenomena is applied the term *phenology*. Phenological indicators are best known for the spring, and the best known of these are flowering of plants, bird migration, and break-up of ice in lakes and rivers (Wing, 1943c). Less well known are insect emergence, fish spawning, and other seasonal events.

Phenological indicators show a spring progression at an accelerated rate as the season advances northward. In like manner, an acceleration occurs along western sides of continents as compared to the eastern side (Hopkins, 1938). The relative earliness of spring may be shown by reference to phenology. Thus, a bird that nested April 10 one year and April 11 the next nested earlier by one day as measured by the calendar. But if the season were 5 days later on the second year, the April 11 nest day becomes phenologically 4 days earlier. The summer, fall, and winter seasonal progress can be measured in a somewhat similar way, though techniques for marking the progress of winter are rather scarce.

Influence of Light. Birds, with but few exceptions (e.g., Strigiformes, Caprimulgiformes), are wholly diurnal. Their eyes accordingly have a nearly pure cone retina which provides keen daytime vision. In addition, red droplets (page 78) aid vision during the sunrise and sunset hours when light rays are red from the Rayleigh effect. The orange droplets act during morning and afternoon, and the yellow ones at midday.

Most birds begin activity at or near sunrise and cease at or near sunset, though regular daily body rhythms related to photoperiodicity continue (Bissonnette, 1937). The time birds cease singing at night or begin in the morning bears a fairly direct relationship to light intensity; morning song will be later on cloudy or cool than on warm or clear days (page 333). As the season advances, morning song becomes progressively earlier, evening song progressively later (Fig. 11·5). The Wren (*Troglodytes musculosus*) began its song at light intensities of 0.5 to 1.4 foot-candles. The American Robin in Tennessee ended its evening song when the light ranged from 0.1 to 10 foot-candles, the Mockingbird between 0.1 and 176.8. Bronzed Grackles in Ohio are reported as leaving the roost when morning light reached about 14 foot-candles and Starlings at about 7.5. Lone Grackles not part of the social group left their roosts at lower light intensities than their fellows in flocks. A study of Herons at a New Jersey roost determined that Little Blue Herons, American Egrets, and Snowy Egrets *arrived* between 16 and 9 minutes *before* sunset, and Green Herons between 7 and 14 minutes *after* sunset. The Black-crowned

Night Heron *departed* between 16 and 19 minutes after sunset. In the morning the same sequence occurred in reverse (Seibert, 1951).

On cloudy days when the light intensity is low, birds may carry on activity all day long in a manner similar to the activity of morning and evening. Studies during solar eclipse show that the light intensity drop brings on evening song and even roosting, though the hour may be midday.

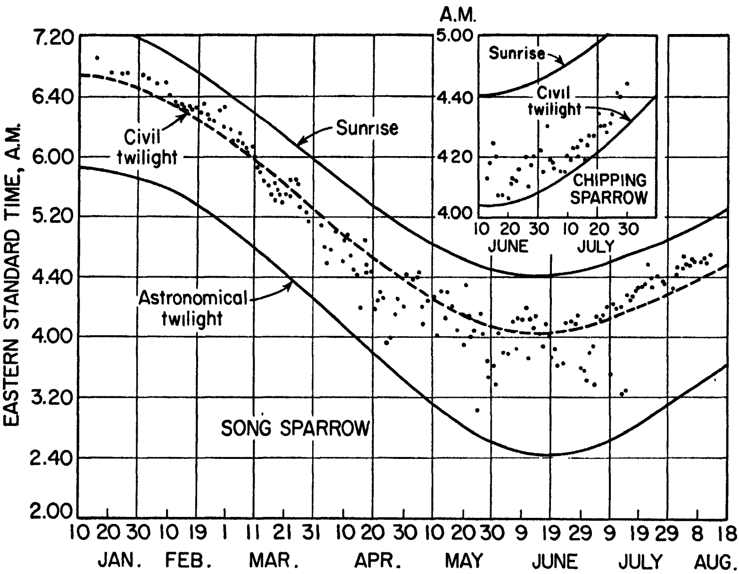

Fig. 11·5. *The time at Washington, D. C., of first morning song of the Song Sparrow and Chipping Sparrow. (After H. A. Allard, "The First Morning Song of Some Birds of Washington, D. C.: Its Relation to Light,"* American Naturalist, *64(1930):436–469.)*

Light influences the habitat activities of many birds. Song Sparrows avoid dense foliage and heavy canopies, though they forage in dark crevices, under stream banks, and under piles of vegetation that cast small shadows. Dark patches of willow have been reported to act as barriers. On the coastal marshes of California, vegetation 2 to 3 feet high will be occupied by Song Sparrows; if only half that high, it will be used by Savannah Sparrows. The latter prefer higher light intensities (Marshall, 1948).

The influence of day length in initiating breeding, migration, and seasonal events is covered elsewhere.

ALTITUDE, MOISTURE, AND WIND

Altitudinal Influences. Marked zonation of vegetation occurs with altitude and with it a reverberation in bird life (Chapter 10 and Figs. 10·7, 10·8). In general, the range of northern birds extends southward in higher altitudes and that of southern species extends northward along valleys. In the same latitude and within a few miles of each other, northern and southern forms will be found, though without ecological overlap.

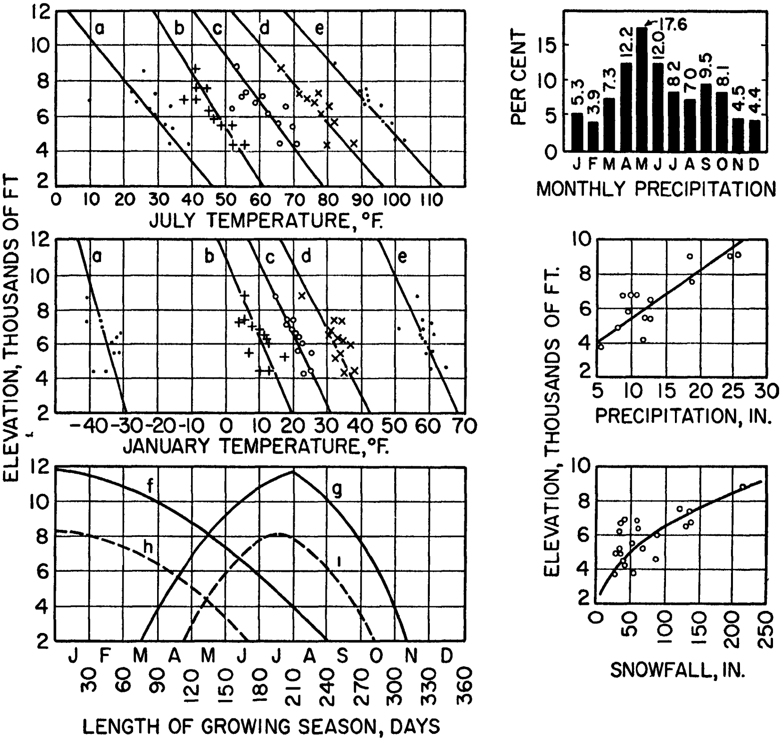

Fig. 11·6. *Climatic characteristics of central Wyoming. (a) Lowest temperature of record, (b) mean minimum temperature, (c) mean temperature, (d) mean maximum temperature, (e) highest record temperature, (f) days of "growing season," (g) start and end of growing season (mean above 42° F.), (h) days frost-free, (i) dates of last spring and first fall frost. (After Frederick S. Baker, Mountain Climates of the Western United States,* Ecological Monographs, *14(1944):223–254.)*

The most marked effects of high altitude upon birds are those of temperature, precipitation, and wind. The season may be short even in low and middle latitudes, for mountain climates vary with altitude (Fig. 11·6). High light intensity may be important also in clear mountain and plateau regions. The Mount Everest Expedition of 1924 noted that small birds spent much of their time in the protection of boulders and depressions to avoid the fierce winds (Hingston, 1926). Many of the birds concentrated around the native villages where protection from wind was available. A few lived in the entrances to burrows of mouse hares. The Redstart nested at 17,000 feet and the Lammergeyer soared at 20,000 feet.

Probably important physiological adjustments to pressure occur in birds, but of this we are relatively ignorant. It is reported that the heart, especially the right ventricle, of mountain Ptarmigan is larger than that of lowland ones. Birds of high altitudes may have greater wing surfaces in proportion to body size than those of lowlands. Trees become gnarled, weatherbeaten, and shrublike near timber line. Often a tree forms a mat that may be but a few inches or a few feet high though many feet across. Exposed trees that grow erect usually have the branches sheared off to windward and tail-like to leeward. Around and under these, small birds such as the White-crowned Sparrow seek shelter. Even the White-tailed Ptarmigan prefers boulder-strewn mountain slopes to open ones.

Similarity Between High Altitude and High Latitude. The conditions of high altitude result largely from cold and often may be desert-like. For general purposes, the high latitude and high altitude effects are alike, though the altitudes have high light intensity and high solar radiation in contrast to polar regions. The plants of mountain slopes in general are related to those of high latitude. The rarefied and clear atmosphere of high mountains (excepting cloudiness) admits more radiation than the atmosphere of lower slopes. This is especially noticeable with ultraviolet rays. The glare of sunshine upon snow in winter may bother birds as well as man, though by nature they may be better able to withstand it.

Moisture and Humidity Influences. Because moisture determines how fruitful the land will be in entrapping solar energy, abundance and distribution of birds vary with moisture and humidity. Birds of the dry, desert regions tend to nest on the east and northeast sides of plants, which provide sun for the morning chill and shade in the afternoon heat. (As birds usually construct nests in the morning, this may only reflect construction-hour choice.) Within the desert, birds seek the thicker and more shade-producing shrubs during the heat of the day, so that a rhythm of movement may occur. Such protection reduces moisture loss.

Though birds must contend with desiccation and heat in dry lands, they profit by the greater freedom from parasites, viruses, and other organisms of sickness. Disease becomes more important toward the wetter and warmer ranges, climate toward the drier and colder ones (page 400).

Drought. Drought influence on birds occurs most frequently on the humid side of the dry lands in the middle latitudes. Another zone of importance may occur near the Tropics of Cancer and of Capricorn. In historic times, drought conditions of the continental interior in North America have resulted in drying of marshes and pools, particularly on the prairies. Drought in the season of young Waterfowl may leave them stranded, though adults can move out. The hatching success of many eggs is usually lower during periods of drought than in normal times.

The production of seeds, fruits, and insects falls off during drought; green vegetation declines also. Many plants produce little food during drought periods and may even skip a crop year. Vegetation upon which birds depend during the nesting season may fail to reach the proper state and nesting may be poor. In the summer of 1951, for example, after nearly 2 years of drought in northeastern Mexico, the thorn shrub vegetation failed to leaf out and flower in a normal manner. In consequence, the great nesting colonies of White-winged Doves failed to materialize, and the birds failed to breed. Only a small portion of the birds came to the nesting sites in April, few birds came into breeding condition, and fewer built nests and laid eggs.

During drought, emigrations of desert birds have been noted, such as of the Sand Grouse of Asia. But desert birds more usually react by remaining within their customary range and declining in vigor, reproduction, and activity (page 92).

Reaction to Wind. The reaction of birds to wind has so important a role that it has been covered in previous discussions of other influences. Little need be said except by way of summary and addition. The individual bird flies lower during wind, perhaps to take advantage of the slowing of wind by surface friction. Birds of weaker flight remain in bushes and trees, but powerful fliers may venture forth in heavy winds. Land birds rise into the wind and turn into it to alight. Water birds do likewise, though they may patter along the surface before becoming air-borne.

Some sea birds nest on exposed sites because of the aid provided by wind in getting into the air. It is said that a level surface with a steady wind is preferred by the guano birds of Peru for nesting. Some sea birds live in windy zones because they perhaps depend upon wind currents for travel. Albatrosses and others avoid zones of calm and follow the oceanic wind belts. Some sea birds possibly may circumnavigate the globe in the Southern Hemisphere by following planetary winds.

Soaring birds, such as Hawks and Vultures, depend upon winds as well as up-drafts of air. Along the sea coast, birds may travel on the on-shore winds or along the up-draft from waves. The winds rising over ridges have been used by migrating Hawks. Hawk Mountain in Pennsylvania derives its fame from this fact. A number of peninsulas concentrate birds in a similar manner (page 308). Migrating birds drift with the wind, as explained in the chapter on migration. A number of sea birds have been carried far inland by riding the winds of tropical storms. Some land birds likewise appear far off their pathways because of wind and storm.

The day-to-day life of the bird may be subject to wind action. Flimsily constructed nests, like those of the Mourning Dove, may be destroyed in numbers by high winds; at times this may be an important if not the most important limitation to nesting success. Birds feed on the lee side of woods and brush during high wind; often they become inactive altogether until the wind dies down. Ground nesters build in vegetation for wind protection, but the Short-toed Lark of Tibet builds a rampart of pebbles on the exposed side of its nest for wind protection (page 216).

SUGGESTED READING

ALLEE, W. C., ALFRED E. EMERSON, ORLANDO PARK, THOMAS PARK, and KARL P. SCHMIDT, *Principles of Animal Ecology*. Philadelphia: W. B. Saunders Co., 1949.

CLEMENTS, FREDERIC E., and VICTOR E. SHELFORD, *Bio-ecology*. New York: John Wiley & Sons, Inc., 1939.

DICE, LEE R., *Natural Communities*. Ann Arbor: University of Michigan Press, 1952.

*ELTON, CHARLES, *Animal Ecology*. New York: The Macmillan Co., 1936.

HESSE, RICHARD, W. C. ALLEE, and KARL P. SCHMIDT, *Ecological Animal Geography*. New York: John Wiley & Sons, Inc., 1951.

KENDEIGH, S. CHARLES, *The Role of Environment in the Life of Birds*. Ecological Monographs 4(1934):299–417.

*LEOPOLD, ALDO, *Game Management*. New York: Charles Scribner's Sons, 1933.

OOSTING, HENRY J., *The Study of Plant Communities: An Introduction to Plant Ecology*. San Francisco: W. H. Freeman Co., 1948.

ODUM, EUGENE P., *Fundamentals of Ecology*. Philadelphia: W. B. Saunders Co., 1953.

WEAVER, J. E., and F. E. CLEMENTS, *Plant Ecology*. New York: McGraw-Hill Book Co., Inc., 1938.

*WING, LEONARD W., *Practice of Wildlife Conservation*. New York: John Wiley & Sons, Inc., 1951.

12

Territorial Relations of Birds

In the folklore of the ancients, the spatial needs of birds and man alike very evidently assumed significance. Even though they had not the benefit of today's fund of knowledge (which tomorrow may seem scanty), observational ability among earlier peoples was not lacking. They demonstrated this in the sage saying that, "No bush will hold two birds and no roof can cover two women." We can hardly do better today, for it recognizes that wild birds and civilized man are two of the most territorially conscious of organisms. Like many other concepts of biology, that of territory may be interpreted often in writings of an earlier day, just as in its folklore. But it would be folly for us to overlook the possibility that we today read ideas that were not theirs into the words of earlier people.

Historical Development of Territorial Concepts. In writing of natural history in 1622, Olina (as reported in 1678 by John Ray) wrote: "It is proper to this Bird at his first coming to occupy or seize upon one place as its Freehold, into which it will not admit any other Nightingale but its mate." Olina, be it noted, added to this the words, "in which it ordinarily sings," though John Ray omitted them (Nice, 1941b). The Swan-herders of Olina's time also recognized territory, for the Swan laws and regulations took note of the territory of the male in the quaint words forbidding interference with a Swan that "hath a walke." Gilbert White mentions bird territory in his famous *Natural History of Selborne* (1789). In 1774, Oliver Goldsmith even used the word *territory* in discussing birds.

Many another writer on natural history mentioned territory, usually in speaking of a single species, clearly in recognition of the spatial needs of birds. Bernard Altum in 1868 discussed bird territory and wrote more completely of it than his predecessors (Mayr, 1935). He elaborated many principles of territory, most of them acceptable today. In this, at least, he went beyond his fellows who recognized the territorial demands of the birds they observed but who did not discuss territory as a principle. The organization of territory as a controlling principle of bird life must be credited to an English ornithologist, H. Eliot Howard, who marshaled the basic concepts upon which others have built.

The Definition of Territory. Though *territory* seems clear enough as a literary word, its use as a technical word in bird study has resulted in inevitable confusion of meaning. Some observers have defined territory as "an area occupied by one male of a species which it defends against intrusions of other males of the same species and in which it makes itself conspicuous" (Mayr, 1935). Certain other terms seem necessary to clarify the concept of space occupied by birds. The area over which an individual moves regularly will be considered here as its *activity* or *home range*, which again is irrespective of age, sex, season, or place. It is likely that use of activity range for the area over which a bird wanders may not be understood by all, but this use of the term *range* is common in parts of the American West. It has the distinct advantage of applying as a general term to the space used by a bird. Its activity range is all the area that it uses regularly, its territory the defended part of this range. At times the territory and range will be the same, but the territory of a colonial sea bird may be only a square yard at its nest, though its range may cover 100 square miles and more. The territory of a Mourning Dove may be only 2 square feet around the nest, though its range may extend 30 miles to a water hole. The *neutral ground* and *feeding ground* are part of a bird's range, though not part of its territory. In an analogous way, the daily travel of a man to and from work covers much of his activity range, though the territory of highly territorial man may be only his house and lot and a few square feet of desk space at the office. The Common Law recognizes that "a man's house is his castle," which merely gives social and legal recognition to the principle of territory as a biological attribute of man.

Kinds of Territory and Range. The breeding habits of birds often govern largely the types of territory taken up. But exceptions occur, particularly in species that maintain a semblance of territory the year around. Some Mockingbirds regularly maintain winter territory, which often may be the same as that of the breeding season. Hence, breeding habits may not always determine the taking up of territory.

"Winter territory" may be a flock territory, as happens sometimes in resident species that assemble into winter flocks, but *flock range* may be a better term. Territory may occur perhaps among birds in migration, though this is still not clear.

A basic classification of territory follows:*

Breeding Territory
  Prenuptial display
  Pairing and pair maintenance
  Copulation (as among Sage Grouse)
  Nesting
Feeding Territory
Seasonal Territory
  Winter
  Roosting
  Transient

A species may have territories that seasonally, sometimes simultaneously, belong in more than one category. Communal territory (as reported in the Ani and Jackdaw) appears similar to the territory of a single bird or pair except that the group defends the territory. "Winter territory" of a Quail covey may likewise be "defended" by a group.

Some types of territory do not as yet fit into any of the several classifications suggested. Perhaps all gradations occur between types.

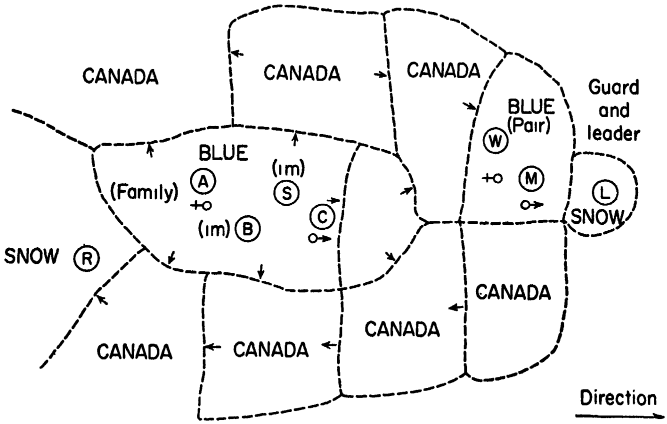

Fig. 12·1. *Territories of Geese when moving (the letters indicate individuals). The boundaries of such "moving territories" persisted when the group moved. Birds low in peck rights stayed in the rear. (After Dale W. Jenkins, "Territory as a Result of Despotism and Social Organization in Geese,"* Auk, *61(1944):30–47.)*

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* Armstrong (1947) discusses the various territory classifications proposed.

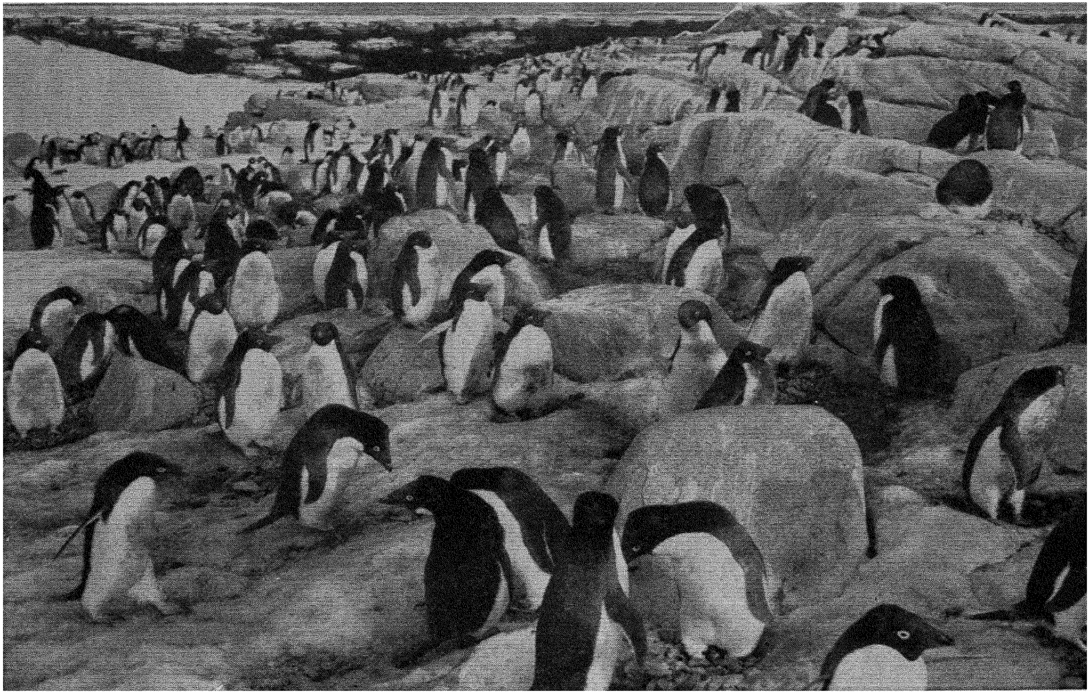

Fig. 12·2. *A colony of Penguins at Red Rock Ridge. The territorial demands of sea birds often have been reduced to little more than the nest and the space within reach of the bill. The restricted nesting islands and headlands thus may serve hundreds of large sea birds within an acreage used in the forest by a single pair of Warblers. (From United States National Archives.)*

Thus the living space of the Cowbird seems to be rather indefinite, though a pair may become dominant over others (Laskey, 1950). Our understanding of the space program of the Cowbird, however, is rather incomplete (page 235). Of unusual interest seems to be the space claims of some captive flocks; birds of a mixed flock of Geese have been reported to move with each bird occupying a particular moving position (Fig. 12·1).

Territory in Colonial Birds. Birds nest in colonies for a variety of reasons, though no clear ones can be ascribed to some colonies. Sea birds particularly nest in colonies, which habit seems to have originated in the physical scarcity of suitable rocks, headlands, islands, or cliffs. A reduction in territorial aspirations by the individual thus seems to be an advantage to the race living where a single island may serve for nesting by the birds inhabiting large ocean surfaces (Fig. 12·2).

Land birds whose habits make suitable nesting sites rather limited in number are those that occupy rocks, cliffs, or banks (e.g., Bank Swallows and Rock Doves), marshes (e.g., Red-winged Blackbirds), and buildings, a substitute for a rock cliff (e.g., House Sparrow, Starling, and Barn Swallow). Perhaps the colonial nesting by Great Blue Herons and Boat-tailed Grackles reflects an ancestral trait of marsh birds. But colonial nesting by some birds, such as tropical Weaver-finches or the Passenger Pigeon of eastern North America, is not so readily explained. A very definite need for complete examination of the subject clearly is in order.

The advantage of a reduction in territorial desire by many birds to the small surroundings of the nest manifestly has an advantage to the race (Fig. 12·3). From the standpoint of the race the Kingfisher with its small amount of feeding room along a creek may safely keep a bank to itself. But Bank Swallows roaming the countryside would not be able to use all of the great feeding space open to them if one pair monopolized a cut-bank. It seems obvious that one pair does not need a whole bank to itself.

Seasonal Territory. The principal seasonal "territory" outside the breeding season is the winter individual range. The Ruby-crowned Kinglet may occupy a dooryard for a few days during migration and drive others away. The American Sparrow Falcon and Loggerhead Shrikes even in migrations show a spacing of individuals. But such spacings and intolerance, though rather common, perhaps should hardly be called territorial.

The more solitary birds show a tendency sometimes to hold a winter "territory," though this may be merely a place where they

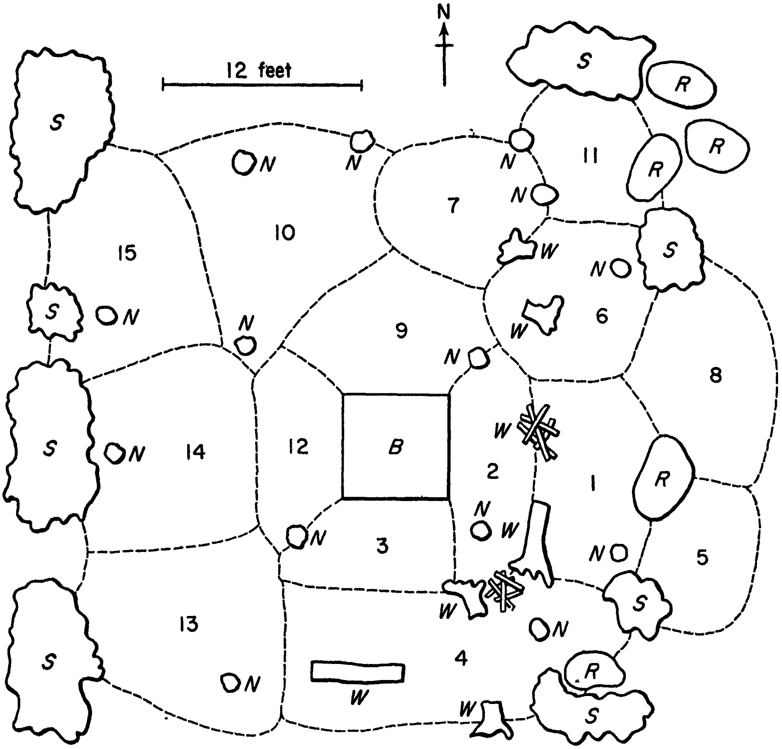

Fig. 12·3. *Map of Herring Gull Colonies, Hat Island, Green Bay, Wisconsin. B, bird blind; S, shrub; R, rock; N, old nest; W, driftwood. (After Murl Deusing, "The Herring Gulls of Hat Island, Wisconsin,"* Wilson Bulletin, *51(1939):170–175.)*

stay by habit. A Blue Grouse may stay alone in one dwarf Douglas Fir but at times two may use the same one. White-throated Sparrows living in a brush patch may be rather intolerant during mid-winter. English Robins have been reported to be similarly intolerant toward intruders in their winter territory (Lack, 1946). The winter territory of the Mockingbird has already been mentioned. Because of the indefinite nature of winter holdings, many writers prefer "winter feeding range" to winter territory.

The roosting spot of a bird sometimes becomes relatively fixed; it may thus be considered as a special kind of seasonal territory. A Starling may return to the same spot on a branch; if several birds are removed, vacant spaces on the roost show their absence. Possibly

American Crows also occupy the same sites at the roost; in any event, the entire roost forms a flock territory for the time being.

Function of Territory. Territory probably serves several functions, its chief one in the breeding season being to aid breeding success. It may be argued with every evidence of truth that it has a survival value or it would have dropped out of the birds' make-up ages ago. Various ways in which territory operates have been put forward by field students. The psychological advantage gained by the bird on familiar grounds enables it to be dominant in its own territory. The pairings-off of birds may be more likely to succeed if one remains fixed and advertises as the male does, so that searching females have less trouble to find a mate. Probably the reduction in strife between birds, brought about by isolation on respective territories, aids breeding success. No doubt also, the protection of the individual, the nest, and the young by ownership of territory and exclusion of rivals or competitors is an important defense point. Nonmated birds presumably would interfere more with the sexual bond were it not for territory.

Territory acts as a population limit in some species, though to what extent has not been established (page 228). The ultimate population will be governed in territorial species, however, by the number able to breed—those successful in getting territories. In this respect, it prevents overpopulation and the resulting destructive forces. The average territory of a breeding bird seems to contain more possibilities for food and nesting than are actually needed. The food supply is guaranteed in normal seasons for a growing family when a territory is taken up. The carryover of territorial claims into winter perhaps may in part express habit, it has been suggested, just as humans find it easier to do repeated acts in the same way rather than to make new decisions.

Selection of Territory. In general, the male bird selects the breeding territory. In the case of migratory birds, the male usually arrives somewhat earlier than the female, and males have territory in various stages of establishment by the time the females arrive. In the Phalaropes, the reversal of sex habits carries over to the territory, which the female establishes. Among our common birds, the males that arrive first start to establish territories. Males arriving later often find the space divided up, so that they must strive to carve out territory from existing holdings, which usually are larger at the start than needed. Older males returning to their previous territories seem highly successful in ousting claim jumpers. Only males in breeding condition establish territories, though exceptions have been reported. Young birds await maturity before establishing territory, as occurs in those that take two or more years for development, but newly mature birds are less successful than others. In species that pair on the wintering grounds, or en route, members of a pair may participate in establishing a territory.

Usually the male defends the territory against intruding males only. Sometimes the female defends against intruding females, but a pair may defend the territory jointly. The females of Yellow-headed Blackbirds, a polygamous species, have been reported to take up a sort of subterritory within the territory of the male. In this species, the respective females maintain these subterritories against each other (Fautin, 1940). The Ring-necked Pheasant uses a similar subterritory system (page 349).

Territorial Boundaries. The boundaries of territories shift considerably early in the season and may shrink very much before becoming static. The female seems to have to learn the boundaries, and much effort by the male early in the season may be directed toward keeping her at home.

Boundaries sometimes follow recognizable physical or vegetational features. One Vesper Sparrow may occupy the land on one side of a fence, another the other side; and the posts may be shared or contested. A creek may separate the territories of two Song Sparrows, a hedgerow those of Mockingbirds, and a row of trees those of Meadowlarks. But often less clearly defined markers may serve. The boundary between the territories of two American Robins may pass across an open lawn, and one Meadowlark may use one side of a tree for singing, while another bird uses the other side. No doubt the birds learn to recognize the boundaries, even though they may be rather more unstable early in the season than they are later.

Defense of Territory. Birds defend territory usually against others of the same species. Defense of territory, as has been said earlier, rests mostly with the male, though he may not be antagonistic toward intruding females (in which case the female may be). In general, the size of the territory may depend upon the ability to defend the boundaries. When birds of a species are less abundant, territory of an individual of that species is large. But increase in abundance tends to bring on more territorial defense than a bird can handle, and the territory shrinks accordingly.

Territorial defense largely involves display and posture, usually by "intimidation," but failure of the intruder to retreat subjects it to physical attack (Figs. 12·4, 12·5). Early in the season the owner may be evicted by the intruder, but this seldom happens later. The owner pursues the intruder to the boundary and perhaps beyond. In case of neighbors, pursuit into the home territory of the intruder brings about a reversal and the pursued becomes the pursuer, which exemplifies the rule that "a male on its own territory is undefeatable" (Tinbergen, 1936). Defense display involves puffing up the feathers, swaying, posturing, or turning color patches toward an opponent. Often threatening sounds accompany display; rushing back and forth may also be part of the performance. In general, the defense action is rather stereotyped for the species, though some individual modification may be in order (Fig. 12·4).

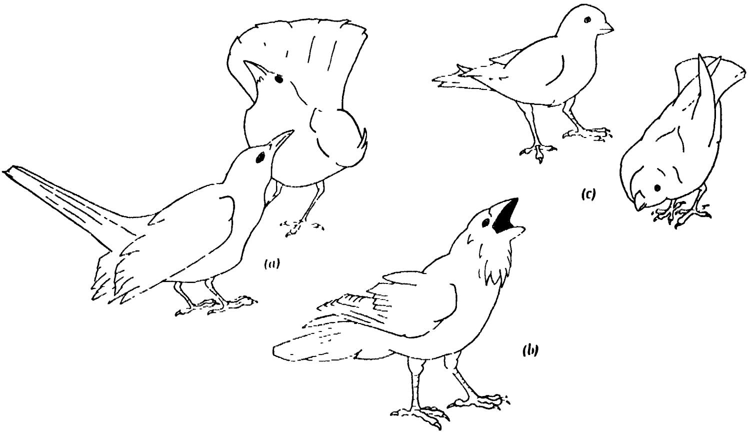

Fig. 12•4. *Display and dispute.. (a) English Blackbirds disputing territory, (b) Raven threat display, and (c) Jackdaw submission display. (Adapted by permission from* Bird Life, *by Edward A. Armstrong, pp. 29, 35, 51. Copyright, 1950, Oxford University Press, New York.)*

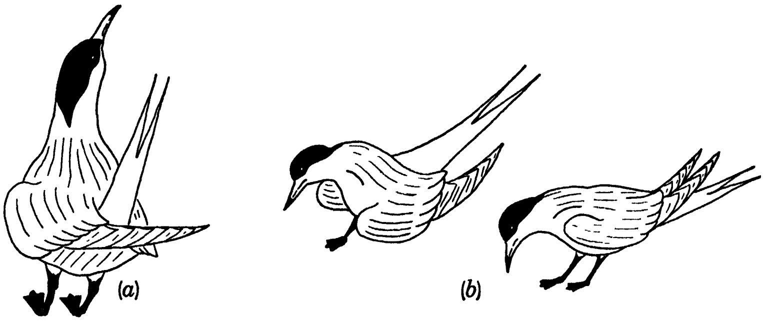

Fig. 12•5. *Common Tern. (a) Threat posture by male to female, (b) threat posture of defending male at nest (left) to intruding male (right). Note the greater active threat position of the owner. (After R. S. Palmer, "A Behavior Study of the Common Tern,"* Proceedings of the Boston Society of Natural History, *42(1941):1–119.)*

Song and Territory. Because Chapter 17 will be devoted to song, it need be covered here only as it clarifies knowledge of territorial activities. Song serves a number of territorial purposes, the chief one being the advertisement of possession by the male. In so doing, it notifies females of the presence of an unmated male and signifies to other males the presence of an occupied territory. The male Bobwhite ceases to sing when it acquires a mate, but a widowed male will sing again.

Territories bereft of their owners usually will be occupied again in short order, probably in early morning (page 257), with subsequent territories tending to be in the same places as those of the predecessors. This substantiates belief that the habitat itself is all-important in explaining local bird distribution. The new males show a characteristic behavior pattern, distinct from that of established owners; the songs are louder and uttered more frequently, and the birds are more active in inspecting their newly acquired domains (Stewart and Aldrich, 1951). Song differences probably signal the state of affairs on the territory; human beings can recognize some meanings of songs and calls, though much remains unknown.

Identification of Territory Limits. Boundaries usually may be identified by watching for boundary disputes and by following the daily travels of the birds, especially those of the males. The male moves about over his territory and by his songs an observer can locate his general territorial limits, but the decisive action always remains the boundary dispute. The various daily movements, actions, and disputes, when mapped, outline the freehold. In intensive studies, the birds may be trapped and marked for later identification as individuals. In most cases, repeated daily observations are needed before territorial limits can be identified with certainty.

Size of Territory. Territory varies greatly in size among birds, and few general rules have yet been suggested. In noncolonial birds, it is said to increase with size of the bird itself. It tends to be larger among predators than among nonpredators, and larger for desert and grassland birds than for brush and forest ones. But it is not possible to compute the size of territory by dividing the total area by the number of pairs, because territories may be set in an "unoccupied matrix" (see, for example, Fig. 11·2). Table 12·1 lists a few examples of sizes of territory reported.

Territory and Population Limitation. Paradoxical though it may seem, territory appears to limit population to the number of possible territories on the one hand and to assure the habitat needs of a capacity population on the other. It has been said that territory is one of the

Table 12·1
Examples of Territory Size in Birds

Species	Area (Acres, or as stated)	Reported by
English Robin	2/5–2	Armstrong, 1950
Ovenbird	¼–3	Armstrong, 1950
Yellow Wagtail	1⅓–5	Armstrong, 1950
European Wren	6–7	Armstrong, 1950
Song Thrush	3¾ or less	Armstrong, 1950
Willow Warbler	⅓	Armstrong, 1950
Reed Warbler	200 sq. yds.	Armstrong, 1950
Golden Eagle	Several square miles	Armstrong, 1950
Black-headed Gull	7 sq. ft.	Armstrong, 1950
St. Kilda Wren	3,000–5,000 sq. yds.	Armstrong, 1950
Zanzibar Red Bishop	900–1,000 sq. yds.	Armstrong, 1950
Song Sparrow	¾	Armstrong, 1950
Yellow-headed Blackbird	1,294 sq. ft.	Fautin, 1940
Mockingbird	1	Original data
Wren-tit	½–1½	Lack, 1946

controls at the top of the food chain (page 443). The total breeding population will not exceed the number of territorial birds that can establish territories, though a floating reserve of unmated birds will exist and also have to be supported by the land. In the final analysis, territories (and hence the breeding of the species) are found only where the habitable holdings provide living needs. Because the size of the territory shrinks as the population increases, yet only to a lower limit (saturation point), it may measure roughly the capacity of the land to support a certain species (page 211).

SUGGESTED READING

*ARMSTRONG, EDWARD A., *Bird Display and Behavior.* London: Lindsay Drummond, Ltd., 1947.

*ARMSTRONG, EDWARD A., *Bird Life.* New York: Oxford University Press, 1950.

HOCHBAUM, H. ALBERT, *The Canvasback on a Prairie Marsh.* Washington, D. C.: American Wildlife Institute, 1944.

HOWARD, H. ELIOT, *Territory in Bird Life.* New York: E. P. Dutton & Co., Inc., 1948.

*LACK, DAVID, *The Life of the Robin.* London: H. & F. Witherby, Ltd., 1946.

*NICE, MARGARET MORSE, *The Watcher at the Nest.* New York: The Macmillan Co., 1941.

NICE, MARGARET MORSE, "The Role of Territory in Bird Life," *American Midland-Naturalist,* 26(1941):441–487.

NICE, MARGARET MORSE, "Studies in the Life History of the Song Sparrow," *Transactions of the Linnean Society of New York,* 6(1943):1–328.

13

Social Relations and Social Behavior

Although one unfamiliar with the wild might think nature always to be in a chaotic state, a characteristic commented upon by generations of naturalists is its *pattern.* A scientific axiom holds that in nature, patterned behavior betokens the operation of order, not disorder; of principles, not accidents; of laws, not chaos. The relationships of the several parts of the body show well the action of order in nature. The relations of a bird with its physical environment likewise show order. Of equal interest, the relations of birds with each other—those of the same or of other species—show recognizable patterns. These all are considered loosely as forms of social behavior.

Many activities of birds, such as those of courtship, might well be included in this chapter as forms of social behavior. But it seems useful to include here (somewhat arbitrarily) actions that concern other relations of birds with each other. In addition, a few miscellaneous habits are included, largely for the reason that our knowledge of them does not fit them particularly well for inclusion elsewhere.

DOMINANCE

Social Dominance. Groups of birds staying together by compulsion (as in caged birds), by flock habits (as in the Blue Tit or Bob-white), by communal courtship (as in the Sage Grouse), or habitat concentration (as in feeding areas), may develop a system of social rank. This *social hierarchy* rests upon the ability of one bird to dominate another. Dominance has been defined as the state of affairs in which one bird has "priority" over another; the first bird *dominates* the second. Birds like the Domestic Chicken, when held in close quarters, develop a *peck order.* The top-rank bird pecks chickens lower in the order than itself without return pecks; the second highest pecks all below it, and so on, until the lowest ranking bird defers to all and dominates none. The social order in a flock of White Leghorn hens is illustrated in Table 13·1. Confined birds in close quarters, like chickens, may develop *peck right,* but those with more space may not. A rather similar type of dominance reported in winter flocks of the Black-capped Chickadee is practically unilateral (Hamerstrom, 1942).

Table 13·1
Social Order in a Flock of White Leghorn Hens

Individual	Number Pecked	Individuals Pecked							
BB	8	RG	RR	GG	BR	YY	BY	GY	RW
RW	7	RG	RR	GG	BR	YY	BY	GY	–
GY	6	RG	RR	GG	BR	YY	BY	–	–
BY	5	RG	RR	GG	BR	YY	–	–	–
YY	4	RG	RR	GG	BR	–	–	–	–
BR	3	RG	RR	GG	–	–	–	–	–
GG	2	RG	RR	–	–	–	–	–	–
RR	1	RG	–	–	–	–	–	–	–
RG	0	–	–	–	–	–	–	–	–

Source: W. C. Allee, "Group Organization Among Vertebrates," *Science,* 95 (1942):289-293.

But a common form of dominance is *peck dominance.* In peck dominance, one bird dominates in a majority of the contacts, not completely as in peck right. The association of position and territory seems to play a role in determining the outcome of these contacts. A bird in its own part of a cage or habitat seems dominant. In winter flocks of Black-capped Chickadees, for example, it has been noted that birds later establishing territory near the winter range of the flock stood high in the social order. This may have been because they were older birds or were actually on their home grounds, just as other birds on familiar grounds seem to have high prestige. The health of the bird may also influence its position, as may hormones (Allee *et al.,* 1939).

Age Dominance. In a group of birds, older ones may tend to dominate younger ones, although some immatures may at times dominate older birds. The first hatched in a nest where incubation begins at laying of the first egg have been reported to dominate later hatched ones, a condition that continued. It seems probable that some of the deferred maturity reported for several gallinaceous birds, Red-winged

Blackbirds, and others, may represent age dominance by the older males over the first-year birds, originating perhaps in the low endocrine level of younger birds. On the display grounds of the Sage Grouse, "master cocks" dominate "subcocks" and "guard cocks," though the age relation is not known for certain (Scott, 1942). The greater dominance of the older male has been noted in the establishment of territory (although it cannot be separated from the greater success of the bird in familiar surroundings) from which he usually ousts his younger rival, even though the latter became established ahead of the older bird.

Sex Dominance. Males sometimes dominate the females prior to the breeding season, though the actual forcefulness varies greatly (Fig. 13·1). After the sex bond has been well established, males may appear very solicitous of the welfare of their mates. There may even be reversals of dominance between sexes, as in the Snow Bunting (Tinbergen, 1936). In the everyday life of the pair, shifts of dominance between the male and the female may occur. Some females dominate at the nest. The male Mallard and the male Shell Parakeet are reported to dominate during the nesting period, though the female does at other seasons. In Geese, the female attains the social rank of her mate, and this may be the case also in several other species that flock together as mated birds. Preference of females for more dominant males has been reported in the Gambel Quail, Ruddy Shell Duck, and Domestic Chicken. But the more dominant Domestic Chicken may be trodden less than its subordinates, even though it may be courted more frequently. The entire matter of sex dominance is in confusion and in need of much study, especially in the wild.

Species Association. Although evidence shows preference of one individual in a flock for others of the same species, most of these expressed preferences are toward birds of the opposite sex. Yet the general gregarious attraction for others of their kind forms the basis of the flock.

Among birds of some habitats, such as of the forest, several species associate in seasonal (usually winter) flocks. This may be measured with an associational index (Dice, 1945a) by dividing the number of random samples in which one species occurs by the number of samples in which both occur together. In the Tropics, mixed-species flocks may associate together at various times of the year. Species associations show varying degrees of interspecies dominance. Nuthatches dominate Chickadees and Titmouses.* In western America,

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* A common error among writers is to use *titmice* as a plural for *titmouses*. *Titmouse* comes from the words *tit* and *mose*, the latter from the Anglo-Saxon being the name for several kinds of birds. The name has no relationship to *mouse* or *mice*.

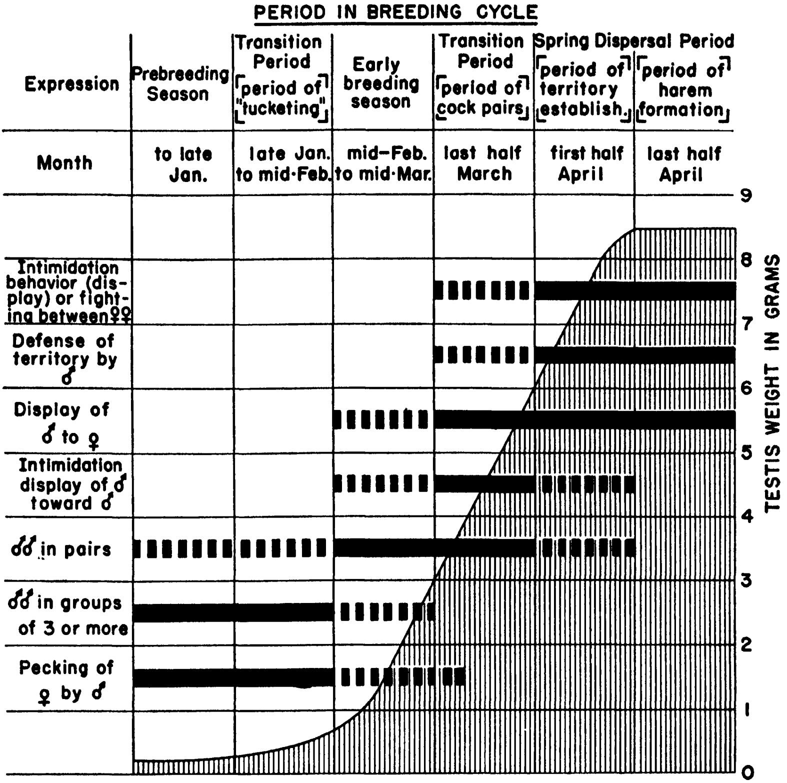

Fig. 13·1. *Display and dominance of Ring-necked Pheasants (January through April). Broken lines represent infrequent occurrence, solid ones represent frequent occurrence. The shaded part of the figure indicates increase in size of testes. (After Nicholas E. Collias and Richard D. Taber, "A Field Study of Some Grouping and Dominance Relations in Ring-necked Pheasants,"* Condor, *53(1951):265–275.)*

the White-breasted Nuthatch dominates the Red-breasted Nuthatch, which in turn dominates the Pygmy Nuthatch. All dominate the Chickadees, but the Black-capped Chickadee dominates over the Mountain Chickadee (Wing, 1946b). The Ringed Penguin dominates both the Adélie and Gentoo Penguins. A male Ringed Plover has been reported to dominate the female Turnstone but to be dominated by the male Turnstone. And a triangular interspecies peck order has appeared among *captive* Cranes, Flamingos, and Pelicans.

SOCIAL PARASITISM

Building nests and caring for the young are so universally characteristic of birds that their absence is noteworthy. Loss of instincts for nest building, incubating, and caring for the young while foisting these duties upon foster parents marks a condition called *social parasitism*. Five separate families of three different orders have evolved the habit, a case of parallel evolution of a separately originated habit. About eighty-six species (not more than 1 per cent of the total of all birds) have the habit. The five families with numbers of species practicing the habit are Waterfowl (Anatidae) 1, Cuckoos (Cuculidae) 70, Honey-guides (Indicatoridae) 6, Icterids (Icteridae) 6, and Weaver-finches (Ploceidae) 3 (Friedmann, 1930). The Cuckoo and Honey-guide families show the most parasitism. More than half of their recognized species have the habit, which probably indicates the ancient nature of its acquisition. Not more than 1 to 7 per cent of the species in the other three families practice it.

Cuckoo Parasitism. The habit of the Cuckoo to lay its eggs in the nests of another bird has been known since very ancient times. Aristotle (386–322 B.C.) commented upon it, and we may feel sure that it was common knowledge. Many writers since the days of Aristotle have written about the habit and offered a variety of theories accounting for it. One student of the subject remarks that the number of theories "became almost as great as the number of writers on the subject" (Friedmann, 1930).

The parasitic habits of the European Cuckoo are better known than those of any other Cuckoo or of any other socially parasitic species. The Cuckoo is a larger bird than its victims, but its egg is about the size of that laid by the host species. The European Cuckoo lays its eggs at intervals of 48 hours, although a few others do so at 24-hour intervals (Baker, 1942). Each strain or race of Cuckoo has been reported to lay its eggs in the nest of a definite species, the eggs resembling closely those of the respective hosts. Cuckoo eggs vary in color from the reddish-brown eggs of strains laying in the nests of Meadow Pipits to bluish-green for those laid in Pied Flycatcher nests. They can usually be distinguished from the host's eggs, however, by their more elliptical shape, slightly larger size, greater weight, and especially by the harder shell, gritty to the touch (Baker, 1942).

The Cuckoo (usually the female?) establishes a territory and watches for nest building by its host species. Nest construction by a victim seems to stimulate egg laying in the Cuckoo, much as nest construction seems to be necessary for continuation of the nesting cycle in the more usual breeding habit. The female removes an egg in her bill, previous to laying her own egg, but not until she visits the nest for laying her own. Once having laid, she pays no further attention to the nest.

The European Cuckoo lays but one egg in the nest of a host species, and its incubation period rather closely matches that of the host species, so that the Cuckoo and the natural young hatch at about the same time. By combination of instinctive behavior and an anatomical depression or cavity in the back (called a "diabolical combination" by one writer), the young European Cuckoo ejects the rightful occupants over the edge of the nest to their doom. The young Cuckoo works itself under the other nestlings during the first few days, before its own eyes are open, and one by one elevates them to the rim of the nest and on over the top. All Cuckoos of species having young markedly larger than their nest mates seem to do this, which leaves the young Cuckoo to be raised alone by the foster parents. Cuckoo species laying several eggs in a nest and with young no larger than the true occupants seem not to have this habit.

American Cowbird. In contrast to the Cuckoo, young Cowbirds do not eject their nest mates from the nest. By sheer bulk, however, the young Cowbird may crowd out the young of small birds. The eggs of Cowbirds are not specialized for each host species, nor do the Cowbirds remove eggs without piercing them. The Cowbird seizes the egg in its bill, the two mandibles making small holes (Chance and Hann, 1942). The Cowbird removes one egg from the nest to be parasitized during the afternoon of the day before laying, less often the day of laying, and rarely the day after. Eggs are removed only when two or more are present (Hann, 1941).

The female watches nest building intently and lays eggs from 1 to 5 days later. She spends from a few seconds to a few minutes at the nest and flies away immediately after laying. Of note is the fact that the Cowbird has developed the habit of laying at early dawn, usually within a half hour of the time that it begins to get light (Fig. 13·2).

The Cowbird lays eggs in "sets" of about five each. This gives three "broods" for the breeding season, which corresponds to the normal successive nestings of other birds. Contrary to general belief, adoption of a parasitic life has not interfered with the mating bond, and Cowbirds practice monogamy (Laskey, 1950).

Origin of Social Parasitism. No satisfactory theory has been devised for explaining the origin of social parasitism. Theories that it originated in polyandrous habits or unbalanced sex ratios (males of parasitic Cowbirds are said to outnumber females) are untenable for

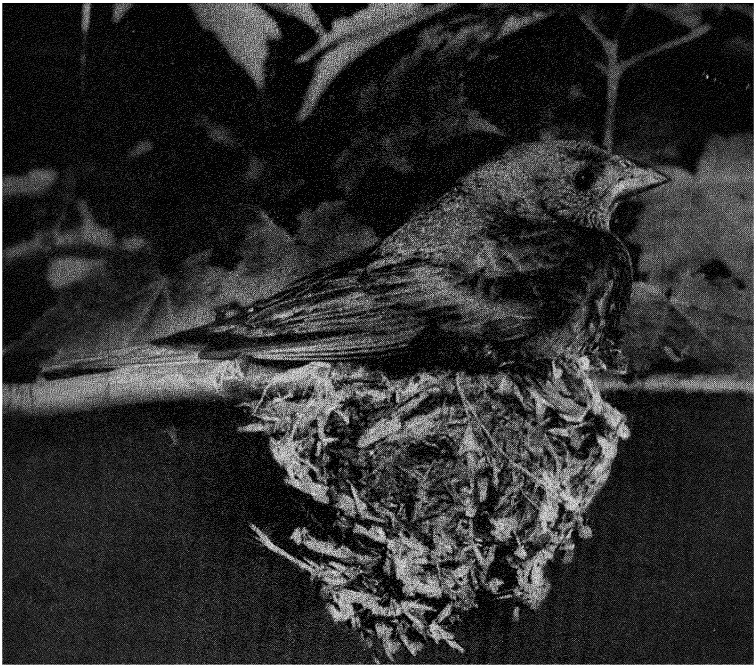

Fig. 13•2. *Cowbird laying in a Red-eyed Vireo nest at 4:45* A.M., *Butler, Pennsylvania, June 11, 1945. (Photograph by Hal H. Harrison.)*

the monogamous American Cowbird as well as for the monogamous *Vidua macroura* (a Weaver-finch of Africa). Usurping a nest has been suggested as an initial stage (page 242). It has been predicated also that the parasitic habit may have arisen from a lack of coordination between the egg-laying and nest-building instincts, resulting in eggs being ready before the nests had been completed. The chance laying of eggs in the nests of other birds by a female stimulated by the sight of the eggs has been suggested also as a beginning of the habit (Allen, 1925), but this must be accompanied by or preceded by a marked reduction in attachment of the bird to its own nest (Friedmann, 1929, 1930).

The Honey-guides, like the Cuckoos, seem to be a family that never had highly developed building habits, which habits would therefore be easier to lose, it is presumed, than highly developed ones. The nest building of the Icteridae, however, is highly developed, as is that of the Ploceidae, both of which have parasitic species. The highly developed nature of the nest building of these two families indicates that the change responsible for parasitism was an internal (physiological) and not an external (environmental) one (Friedmann, 1929).

FLOCKING

Gregariousness. A rather high proportion of birds shows gregarious habits during the nonbreeding part of the year. It can be said with realism that this tendency for gregariousness characterizes the bird.

In the middle and high latitudes, the solitary and "asocial" nature of the breeding season gives way rather early to the flocking of the migration season (page 312), though it may persist over much of the summer. The core of the flock in many small birds seems to be formed by the broods of young that gather in favored feeding areas or wander about to unite with other wanderers. Late nesters appear to be late flockers. Among some species, adult and young tend to flock together, though in others, many adults may be tending to late broods or nests. In a few others, the adults flock together and migrate separately, sometimes ahead of the young.

Male Ducks of the marshes desert the females and band together in summer; these bands seem to constitute a nucleus for later flocks. The birds that have congregated in protected marsh areas for molting of the flight feathers form another nucleus, and the broods of young make up still a third. Among Geese, Swans, and Cranes the family stays together but joins with others for migration, so that a flock of such birds may become an aggregation of family units.

The role of preference for familiar birds ("friends") and of *site tenacity* in holding flocks together is not known. It has been shown that some birds know each other as individuals (page 348). But colonial birds may form rather fixed nesting groups because of site tenacity, a behavior trait of the Common Tern modified by another, trait termed *group adherence* (Austin, 1949). The bond holding together some of the social birds, like members of the Weaver-finch family, may be of this nature.

With the advance of the breeding season, the gregariousness breaks down into the isolation tendency of the territorial birds (Chapter 12). Colonial birds show much less of this breakdown, being territorial largely in respect to the nest site itself. Some land birds in the nesting season show a definite gregarious tendency not of a colonial nature. But colonial birds clearly show their gregarious nature in the breeding season. The Passenger Pigeon nestings involved millions of birds. Many species of Dove nest in colonies (e.g., White-winged Dove and Red-billed Pigeon) but others may be solitary nesters.

Migrating Flocks. The way in which the flock flies is a characteristic of the species and to some extent of groups. It is related also to habitats. American Robins drift across the sky in loose flocks, while the drift of New World Blackbirds and Grackles is somewhat more compact. But both may string out as far as can be seen. In a sense, they are aggregations of flocks (sometimes called *flights*) rather than an individual flock. Shorebirds tend to form into compact flocks that may wheel about the sky in a "drill formation." As they twist in unison, they often flash light and dark as the light underparts or dark backs turn to the observer. Starlings, Waxwings, and a few other land birds may do so also. Brown Pelicans and others fly in a V-shaped flock, a formation that lets each bird utilize some of the energy lost by the lead bird in forming vortexes off the wings (Storer, 1948). It also gives vision ahead, though this seems not to be an important item.

Size of Flocks. The size of bird flocks varies conspicuously, which probably roughly indicates gregariousness. Birds may *associate* together because of the gregarious urge or *congregate* together for reasons of habitat (Wing, 1941). The former probably constitutes a true flock, the latter a congregation. The smallest size of a flock would be two birds associated together (as distinguished from a mated pair). Two White-breasted Nuthatches in winter show awareness and interest in each other by their calling back and forth, and the two would form the minimum flock.

Table 13·2

Size of Bird Flocks in the Christmas Censuses

Species	Number of Flocks	Number of Birds in Average Flock
Bob-white	1,362	11.9
Downy Woodpecker	407	2.1
American Crow	378	45.2
Black-capped Chickadee	733	6.0
White-breasted Nuthatch	301	2.3
Starling	487	67.3
House Sparrow	394	28.0
Cardinal	354	4.3
Slate-colored Junco	396	16.2
Tree Sparrow	451	18.0
Song Sparrow	326	5.4

Migratory birds gather into larger flocks than resident ones; the flock of semimigratory birds falls between the two. Thus, 6,492 flocks of Passerine birds in winter averaged 18.6 birds for the migratory species, 10.3 for the semimigratory, and 8.0 for the resident ones.* Data for birds with more than 300 flocks each during the Christmas Census season in the United States and Canada are given in Table 13·2.

Size of Flock and Habitat. Birds, like mammals, show greater gregariousness in the open range environment than in the brush or forest. In fact, few birds of the forest ever form large flocks except for those that range widely over the forest canopy or when away from the forest in winter, as shown, for example, by the Bohemian Waxwing. A comparison of 6,283 flocks of small birds at Christmas time indicates clearly the working of this rule of differential gregariousness (Table 13·3).

Table 13·3

Variation of Flock Size with Habitat

	Number of Flocks	Size of Average Flock
Forest birds	2,926	4.1
Brush birds	1,841	8.6
Birds of the open	1,516	16.9

The Bob-white shows a habit, which may be of wider occurrence among birds, of going in larger flocks in the colder parts of its range. The covey averages about a dozen birds (average of 11.9 for 1,362 flocks in the Christmas Censuses). But flocks of the warmer regions average about two fewer than in the coldest part:

North Central	12.5	South Central	11.0
Northeast	11.3	Gulf States	10.8

Among families of North American birds, the Icteridae, Anatidae, Laridae, and Corvidae lead in gregariousness as measured by flock size. At the other extreme, the least gregarious, as measured by flock size, are the Falconidae, Accipitriidae, and Strigidae. The most gregarious species, as measured by winter flock size, seem to be the Cowbird, Red-winged Blackbird, Canada Goose, Starling, American Crow, and Coot. The most solitary are the Northern Shrike, Barred Owl, Screech Owl, Goshawk, Sharp-shinned Hawk, and Cooper Hawk. The most solitary birds are predaceous ones; hunting for prey on land evidently does not lend itself well to flock effort.

Advantages of Flocking. It would seem obvious that an important manifestation of life like the flocking habit would have a most important advantage to the species and to the birds practicing it. Many advantages have been suggested, and doubtless they vary from species to species and from place to place.

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* Original data.

The advantages of flocking to the small prey species as a measure of protection from an enemy seem to be many, though considerations of predator-prey relations tend to overemphasize the role of the predator in the life of the prey. A flock of feeding birds almost always has one or more birds looking up from feeding, who would thus be able to detect and to give warning of an approaching enemy. A predator making a dash into a flock free to escape can become confused by so many similar birds and fail to concentrate enough on one bird to catch efficiently. The response of a flock to the distress call of a bird often is real, and the attacker may be harassed or literally mobbed by his prey. The soaring Turkey Vulture sights another dropping to food, and by following it in turn notifies others so that soon a number from several miles around will be attracted to a dead animal. The Vultures, however, should be considered as essentially solitary in their soaring, though roosting in groups. A Carolina Chickadee finding a suet station for the first time calls in a voice that seems interpretable as notifying others of the food, for others come quickly to it. Foraging by a flock spread out over considerable area gives more probability of locating any food present than if the birds went alone.

A lone bird or a small flock of some species shows a nervousness not found in a large flock, and it may be assumed from this that the normal size flock may satisfy better the gregarious nature. Birds seem to have some facility for judging numbers, for some species almost never travel in small flocks in winter.

Of special interest are the few examples of flock continuity generation after generation. A number of cases have been reported of flocks of birds (such as House Sparrows, in Chapter 20) having an albinistic trait show up for a number of years. Individuals hatched, lived, and died, yet the structure of the flock held together strongly enough to maintain the sprinkling of albinism.

OTHER HABITS

Mutualism. Several habits of birds have been given various names from time to time, such as *cooperation*, *mutualism*, *commensalism*, *symbiosis*, and *alliances*. Thus, the American Cowbird attends upon cattle and horses (but formerly bison) for flies and other insect life. The Cattle Egret of Africa performs a similar duty for the African buffalo and elephant. Several birds of the Shorebird group have been noted to dart in and out of the open mouths of basking crocodiles, but whether to feed upon food remnants, leeches, flies, or gnats has not been established. Ancient writers thought that they fed on leeches as a sort of favor to the reptile. The Ox-pecker, sometimes called also Rhinoceros Bird, feeds around cattle, camels, antelopes, and rhinoceroses of Africa somewhat as do the Cowbirds of America. Occasionally its habit of picking ticks may lead to picking at wounds (perhaps caused by ticks) to bring further injury to the animal. The Rosy Bee-eater of East Africa rides upon the back of the Bustard, evidently using the larger bird as a walking substitute for a bush. From this perch, it sallies forth to capture insects and return to its perch.

Many cases of apparent association of small birds with larger or more pugnacious ones have been reported, though it is difficult to separate intentional association from the habitat preference which throws the birds together. In parts of the American West, nests of the Raven frequently are placed near those of the Prairie Falcon. But a probable explanation may be that the Falcons often use old nests or nest sites of Ravens and other birds, and Falcons and Ravens alike tend to return to the same nesting area year after year. Because cliffs with suitable ledges are necessarily limited in number, some closeness of nesting may be expected.

Small birds have been reported nesting amidst the sticks of larger birds' nests. Some reports seem to show that the smaller bird *seeks* the nest of the larger one, but others indicate that the smaller bird merely selects what proves to be suitable to it, not necessarily because it is a predator's nest. But some birds of the Tropics seem to pick nest sites at or near the nests of pugnacious birds like the Flycatchers. A few may place nests in acacia bushes which are also the homes of acacia ants living in the hollow thorns. But it seems highly improbable that the birds do so in order to take advantage of the stinging of the ants as a defense against possible enemies. One should always bear in mind, however, that bird studies in remote places suffer from their short-time nature.

The habit of the Burrowing Owl to live in burrows in prairie dog towns has long been commented upon. But the harmony of rodents, birds, and rattlesnakes popularly envisioned does not occur. The Burrowing Owl may use a burrow for many years. One in Douglas County, Washington, was occupied by Burrowing Owls from 1902 to at least 1939 (Jellison, 1940).

Highjacking. An activity of some birds in pirating food from the rightful hunters has been called *parasitism*, but a far better term for such brigandage is the American word *highjacking*. The several species of Jaegar and Skua intimidate Gulls that have caught fish and force them to give up the catch. Gulls in turn sometimes highjack fish from Terns and Pelicans. The Frigate or Man-o'-war Bird likewise forces Gannets, Pelicans, Cormorants, and others that catch larger fish to give up the catch, but the Frigate seems to do this largely in calm weather, a time difficult for its type of flying and foraging. The

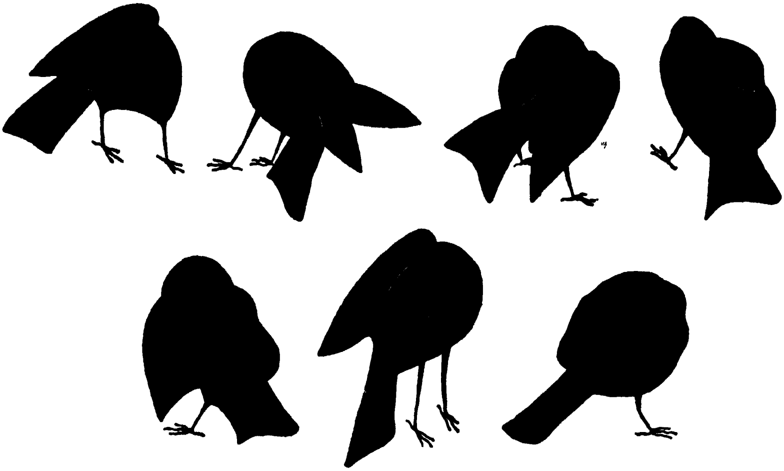

Fig. 13•3. *The act of anting as done by a Song Sparrow.* (*After Margaret Morse Nice and Joost Ter Pelkwyk, "'Anting' by the Song Sparrow,"* Auk, *57(1940):520–522.*)

Bald Eagle feeds upon fish that it catches for itself, but it also highjacks from the Osprey.

Another form of highjacking has been noted in the stealing of nests of birds. Thus, the Horned Owl has been known to dispossess Bald Eagles, Red-tailed Hawks, and American Crows. But among some species, usurping the nest of another replaces normal nest building. The Bay-winged Cowbird of Argentina and other parts of South America nests late, after most other birds have finished, when empty nests that it can use are most abundant. But pairs of Bay-winged Cowbirds frequently fight with other birds and take possession of their nests, ejecting any eggs or young present. In most cases, they do some repair to the nest. If no nests are available, either by piracy or by taking over abandoned ones, the Bay-winged Cowbird may build a nest, which shows that they still possess a latent nest-building instinct brought into play when other means fail (Friedmann, 1930). The Bay-winged Cowbird cares for its own young, but in turn is parasitized by a relative, the Screaming Cowbird. The latter is derived phylogenetically from the former, and the usurping of another bird's nest may be an initial stage in the evolution of social parasitism (Friedmann, 1930).

Anting. Birds have been observed to frequent or bathe in ant hills and to dress their feathers with ants. The act may vary from placing the ants under the wing to actually rubbing the ant into the feathers.

Several substitute actions, some involving pungent berries or other objects, have been reported. The purpose of this action has not been explained, although claimed to be some form of parasite control by the formic acid or other acids in the bodies of the ants (Figure 13·3).

Wing Flashing. Mockingbirds feeding or hopping about a lawn often pause between runs and lift the wings in a performance called *wing flashing* (Sutton, 1946). Females usually practice the act, though rarely will a male do so; young birds hardly able to flutter about a lawn may do so also. No explanation has suitably accounted for this practice. It may be part of a food-gathering performance, an effort to make insects reveal themselves, or an instinctive gesture of wariness. The fact that females and young do most of the flashing has suggested also the explanation that it is some signal appropriate to identification of sex and immaturity.

Similar acts have been reported for the Brown Thrasher, Road-runner, and Least Bittern. That of the Road-runner and Least Bittern seems related to food gathering, though that of the Mockingbird may not be. The related Catbird (possibly only the female and young) have a performance involving a rapid, shivering wriggle of the wings. It appears to be a part of or related to courtship and nuptial display. It has been suggested that the wing flashing of the Mockingbird is a slow-motion analog of this performance.

SUGGESTED READING

ALLEE, W. C., *Cooperation Among Animals.* New York: Henry Schuman, Inc., 1951.

*ARMSTRONG, EDWARD A., *Bird Display and Behavior.* London: Lindsay Drummond, Ltd., 1947.

*ARMSTRONG, EDWARD A., *Bird Life.* New York: Oxford University Press, 1950.

BAKER, E. C. STUART, *Cuckoo Problems.* London: H. F. & G. Witherby Ltd., 1942.

CHANCE, EDGAR P., *The Truth About the Cuckoo.* London: Country Life, Ltd., 1940.

*DARLING, F. F., *Bird Flocks and the Breeding Cycle.* Cambridge, England: Cambridge University Press, 1938.

*EMLEN, JOHN T., JR., "The Study of Behavior in Birds," in *Recent Studies in Avian Biology.* Urbana, Ill.: University of Illinois Press, 1955.

FRIEDMANN, HERBERT, *The Cowbirds.* Springfield, Ill.: Charles C Thomas, 1929.

HOWARD, H. ELIOT, *An Introduction to the Study of Bird Behavior.* Cambridge, England: Cambridge University Press, 1929.

*LORENZ, KONRAD Z., *King Solomon's Ring: New Light on Animal Ways.* New York: Crowell Publishing Co., 1952.

RICHDALE, L. E., *Sexual Life of the Penguin.* Lawrence, Kan.: University of Kansas Press, 1951.

SCHELDERUP-EBBE, T., "Social Behavior of Birds," chap. xx in MURCHISON, *Handbook of Social Psychology.* Worcester, Mass.: Clark University Press, 1935.

TINBERGEN, N., "Social Releasers and the Experimental Method Required for Their Study," *Wilson Bulletin,* 60(1948):6–51.

TINBERGEN, N., *The Study of Instinct.* London, England: Clarendon Press, 1951.

14

Bird Abundance

Like many other words in common use, *abundance* and *population* may mean different things to different people. Both have various shades of biological meaning, some definite but others indefinite. In general, the word population has the more exact meaning in the biological field. Among bird students, it may mean (1) all the birds of a geographic area, (2) all the individuals of a species, (3) the individuals of one or more species in a habitat, (4) an interbreeding group of birds of one species, or (5) a group of individuals forming a subgroup within a species unit, often in a genetic sense.

An important part of any abundance study is the relative numbers of males and females, and of adults and young constituting the whole (Chapter 8). Birds may be of any age from newly hatched young to oldsters. It may be assumed from the practical standpoint that no birds past the breeding age survive long or make up any important part of the population. Figs. 14·1 and 14·2 show sample analyses of populations in the wild.

ENVIRONMENT AND ABUNDANCE

Environmental Population Influences. Any environmental factor that influences survival, presence, or numbers of birds is reflected in the problems of bird abundance. The salinity of ocean water affects the composition and abundance of plant and animal life, which in turn may influence bird life. Because the oxygen of the water, the fertility of the soil, or the temperature of the air controls so markedly the success of the plant and animal life, we can hardly limit consideration of the environment as a population influence or even as a population control. This discussion, however, considers other manifestations and leaves the environmental influences largely to other sections or to the suggested readings.

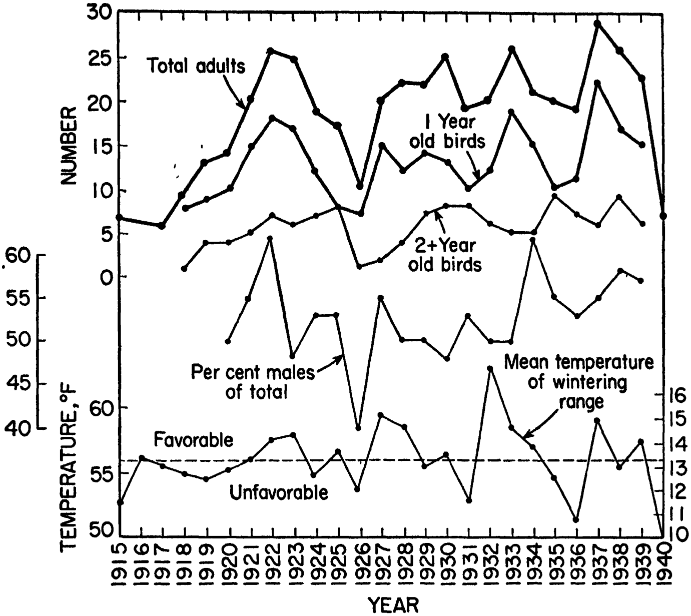

Fig. 14 • 1. *Analysis of the population curve of the House Wren in respect to age and sex and correlated with the mean December–February, winter-range temperature. (After S. Charles Kendeigh,* Measurement of Bird Populations, *Ecological Monographs, 14(1944):67–106.)*

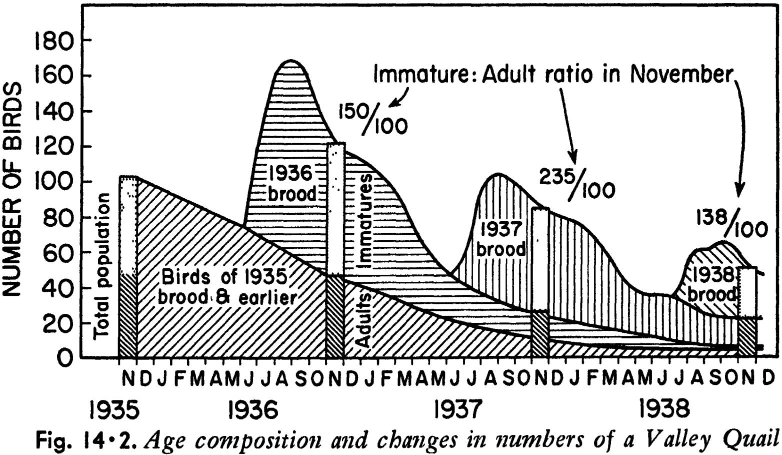

Fig. 14 • 2. *Age composition and changes in numbers of a Valley Quail population at Davis, California, as determined from banding. (After John T. Emlen, Jr., "Sex and Age Ratios in Survival of the California Quail,"* Journal of Wildlife Management, *4(1940):92–99.)*

Population Measurement. There are several ways of determining and indicating bird populations; for most purposes these may be divided into four convenient groups: (1) total enumeration, (2) enumeration by classes, (3) sample counts, and (4) relative abundance counts. As would be expected, the four groups listed are not mutually exclusive. Bird students commonly call counting methods *censuses*, though the term may have somewhat different meanings in other fields.

Ornithologists seldom enumerate all the species of an area or all the individuals of a species except on *sample areas*, which enumerations correctly are considered as *sample counts*. Yet a few such total enumerations can be made on occasion. Bird students in Michigan have made counts of the small population of Kirtland Warblers and conclude that the total number does not exceed one thousand (Mayfield, 1953). A practically total count of the Greater Snow Goose is possible at its resting grounds on the St. Lawrence during fall migration. In the same way, the Great White Heron, Whooping Crane, and several other remnant species may be counted in their entirety. Birds that nest in colonies, such as Herons, Pelicans, Gulls, and many others can be counted if the range is not too large (Fig. 14·6). It is likewise possible to enumerate all the birds of an island or other similar area so as to have a total, not a sample count. Enumerations of this nature result in valuable bird population data.

Enumeration of birds by classes commonly takes the form of sex counts or age counts. Often such counts are obtained as a by-product of some other activity, among which the most common are trapping for banding, checking the game birds killed by hunters, and counting birds in flocks. Successful counting by classes of live birds in the field requires that the birds be distinguishable at a distance. Sex counts of birds in flocks, as in Waterfowl, take two persons, an observer calling off to a recorder (Yocom, 1951). It is possible, however, for one person to count the birds of one sex and then to count the total flock in a second operation.

The commonest sample counts take the form of censuses over predetermined areas. These may be of a single-cover type or of an area embracing several types. Although the taking of counts would seem to be a relatively simple procedure, biometricians indicate that, except for counts based upon territory determination, a rather large number of variables weakens the statistical validity of many of the results.

Relative abundance counts gather data not as total counts but in relation to some unit of time or space (Chapter 24). The commonest ones are birds observed relative to hours, days, weeks, months, field trips, or distance. The data usually appear as *birds per hour* or *birds per mile* or as a *frequency of occurrence*. Relative data may also be obtained by sounds, movement, or other manifestation indicating abundance. Thus, one may make a song count of Woodcocks or drumming count of Ruffed Grouse.

All population determinations are subject to the influence of flocking and seasonal characteristics. As discussed elsewhere, gregariousness reaches its lowest ebb in the breeding season, though even then groups of unmated birds or even late spring migrants will be found. Even the family groups give trouble in field counts, especially in species like the Black-capped Chickadee whose young may not necessarily be distinguishable from adults. Adding to the complexity of the problem are differences as of habits, conspicuousness, cover choice, daily rhythm, seasonal rhythm, and identification ease (Kendeigh, 1944).

Breeding Potential and Environmental Resistance. Every bird has the capacity to reproduce itself, which, on theoretical grounds at least, seems always equal to the loss caused by environmental pressures. The idealized reproductive capacity is termed the *breeding potential* and the reduction features of the environment, *environmental resistance*.

Though we think of the breeding potential as a fixed biological characteristic of the bird itself, some variation does occur. When populations are high, the number of eggs and even the number of broods may average fewer than when populations are low, in accord with the principle of *inversity* or *inverse tendency*. Birds in various parts of their ranges may lay larger or smaller numbers of eggs to a set, or they may nest more often or less often during a season (Chapter 18). While it may be argued that these elements are environmentally induced, it seems best to term them *internal adjustment factors*. The relationship among the three gives the population, which may be expressed as the relationship:

$$P = \frac{BP}{IAF} - ER$$

The breeding potential represents the factors of number of eggs per nest, number of nestings each season, and number of reproductive seasons in the life of the bird. A species that averages four eggs, nests three times a year, matures in 1 year, and whose life averages 4 years (through four nesting seasons) would have a breeding potential of forty-eight for each pair. But one of the same laying capacity and age but taking 2 years for maturity would have a breeding potential of thirty-six for the same years. Environmental resistance foredooms forty-six attempts of the one species to failure and thirty-four of the other. Fig. 14·2 illustrates actual records of the "saw-tooth" nature of the yearly fluctuations in population. Fig. 14·3 shows the concept of an idealized yearly curve of population in a "stable system." If the environmental resistance becomes greater temporarily, population declines; if permanent, the population establishes a new, lower level. Continued increase of environmental resistance (or too great an increase) may mean decline to extinction. A reduction in environmental resistance means an increase in population, permanent or temporary as the case may be. But population increase is self-limiting because of space needs and other internal factors, so that continued increase does not occur for long.

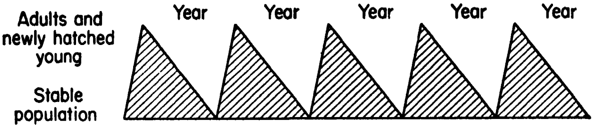

Fig. 14·3. *Idealized curve of population to show the rise to a peak with the arrival of young in the nesting season and decline to previous level at the corresponding period next year. This zig-zag curve is the normal thing in nature (compare with Fig. 14.2).*

Some pertinent generalizations may be made, though we must recognize the limitations inherent in our knowledge of breeding in the wild. The breeding potential in part actually reflects the breeding effort necessary for replacement of the parents (and birds dying without successors), a factor recognized under the general term of *life hazards*. The pair of birds with forty-eight tries would take four years to replace itself, whereas the one with thirty-six tries takes three years. The yearly effort of twelve each is the same and the net replacement the same—the number of parents. Probably a representative measure of the reproductive potential is the net possibilities for a common period of effort, such as efforts needed for a century of reproduction. Both birds in the example would lay 1,600 eggs, one would have twenty-five generations, the other thirty-three. But for fifty generations, the former bird would lay 3,200 eggs and the latter, 2,400.

Table 14·1 indicates possible *egg-success ratios*. It also gives a very real idea of the gaps in our ornithological knowledge. Except for the number of eggs and possible number of nestings each year, the data are largely conjectural. We do not know the number of years of reproductive life; some birds do not mature until the second or third year (perhaps even longer). But the general pattern seems logical, though our knowledge of it will surely improve.

Table 14·1

Possible Expected Egg Success of Birds

	No. of Eggs	Nests Each Year	Laying Seasons	Total Tries	Possible Expected Egg Success
Ducks	10	1	4	40	.05
Geese	6	1	6	36	.06
Cranes	2	1	10	20	.10
Grouse	10	1	4	40	.05
Quails	14	1	3	42	.05
Turkey	12	1	5	60	.03
Hawks	4	1	6	24	.08
Shorebirds	4	1	3	12	.17
Owls	3	1	4	12	.17
Mourning Dove	2	3	3	18	.11
Passenger Pigeon	1	1	5	5	.40
Crows	4	1	3	12	.17
"Passerine birds"	4	2	2	16	.12

In general, it may be said that species laying large numbers of eggs do so because the expected egg success is low. The Passenger Pigeon which laid only one egg, on the contrary, had a high chance of hatching and maturing that egg (and others of its laying life) into a bird to succeed its parents. It is likely that a Crane laying for ten seasons (probably they lay for more) has a potential reproductive success for its eggs not much greater than that of a Passerine bird. But the fact that the young take several years for maturity introduces age-class complications. Age itself increases life hazards, which may be additional factors in low egg-success expectancy. A low turnover perhaps does not supply the "biological vitality" of a rapid one. Such likely variations of success no doubt occur throughout the bird world.

Geographic Variation. Geographic variations in the expected egg success clearly can be seen in the field. The American Robin of the mid-continent lays about four eggs and nests two and often three times a year. But the Robin of the Arctic lives in a land of short summers where one brood may be all that it can raise. In the one case, the pair may lay twelve eggs a year, in the other only four. Since the job of all eggs is the same—replacement of the parents and birds dying without young—the egg-success expectancy of the northern eggs seems to be three times that of the other. We do not know if there are differences in length of life or in life hazards which influence this outcome. A low nest destruction in the Arctic and lower loss of fledglings may be one factor in the difference. Obviously, the low support rate of the Arctic with its low entrapment of biological energy makes a high breeding potential rather less necessary than farther south.

Life Equations. Fig. 14·2 illustrates the principle of *life equations*, which simply means that the gains and losses from season to season balance each other. The number of birds rises sharply in the breeding season (with the advent of the young) to the annual peak; it declines throughout the year and reaches its low point at the start of the next breeding season. Comparable season numbers remain equated with those of other seasons.

Life equations differ from the population equation (page 247) in that life equations concern the year to year gains and losses of a population group. A life equation can be stated simply as follows: The number of birds of one year plus the additions of the breeding season minus the yearly losses equal the number of birds next year.

RESTRICTIVE FACTORS

Limiting Factors. The concept of *limiting factors* used in game management (Leopold, 1933) fits with peculiar aptness into thinking of bird populations. It applies well also to any bird attribute contingent upon ecological relations, such as bird abundance, spread, and distribution. In a broad sense, ecological limiting factors include concepts of the "minimum," such as the "law of the minimum" (Liebig's law), "law of the limiting factor," and "law of tolerance," though these have been elaborated more as principles of "organismal growth" than as population rules.

Limiting factors are the nine intertwined ecological constituents of *productivity* that may be listed for convenience into two groups:

DIRECT FACTORS (DECIMATING)	INDIRECT FACTORS (WELFARE)
Predation	Competition
Starvation	Food and water supply
Disease	Climate
Accidents	Habitat
	Special factors (dust baths, etc.)

The limiting factor is the *one most important at the time in restricting the population.* A factor limiting at one time, season, or place may not be so under other circumstances. The absence of suitable mud for nest retorts (special factor) may be the limiting factor for the Cliff Swallow along a river canyon. Farther along the river, lack of suitable cliffs on which to attach the nests (habitat) may become the limiting factor. Regionally, climate may be the limiting factor, both with respect to population and to species distribution. Year to year variations in the limiting factors, however, may have less influence upon population trends of some birds than their own *density relations* (Errington, 1945).

Predation Relations. Predation and competition are components of environmental resistance which influence bird population in several ways. The predation influence upon the annual mortality of game species depends upon five variables (Leopold, 1933); these seem appropriate to bird species in general when expressed thus:

Density of the bird population
Density of the predator population
Food preferences of the predators
Physical condition of the bird and the escape facilities available to it
Abundance of "buffers" or alternate foods for the predator

Knowledge of the influence of predation upon populations is confused by the fact that it is only one of the agencies of environmental resistance. Birds vulnerable to predation may be the victims of one agency and by that action simply miss becoming the victims of another, so that many types of loss—including loss from predation—are at least *intercompensatory* in net population effect (Errington, 1946). Hence, the picture of wild bird populations rising and falling with increase or decrease of predation seems unreliable, although experimental populations of invertebrates in the confined quarters of a test tube may do so (Gause, 1934). In reality, predation is an energy transfer sequence of the *food chain* (page 443), and we may assume the validity of the empirical rule that no member of an energy transfer system destroys its subsistence base. It seems likely, though our knowledge is only fragmentary, that ordinarily population density relationships play a greater role than predation in controlling population levels. The variables influencing the population may thus be considered as either *density-dependent* or *density-independent* in character (Allee *et al.*, 1949).

Predation studies indicate that the number of birds in excess of the carrying capacity of the habitat form a *vulnerable* group, at least in resident species. Pellet analysis, for example, showed Bob-white remains in 5.6 per cent of Horned Owl pellets when the prey were at 36 per-cent of the winter carrying capacity, and 19.0 per cent when insecure at 141 per cent of capacity (Errington, 1937). The predation rate rose with increase of birds in excess of the number that the land could support adequately.

Competition Relations. Competition may be the spice of life in human societies, but to birds it is a continual scramble from which only the successful emerge to survive or to reproduce. Fundamentally, birds compete directly with each other, though on occasion rivalry may be between bird and mammal or more rarely between bird and other organisms. It seems possible to list competition among birds under three headings:

- Interclass competition
  - For example, between insectivorous birds and lizards for insects or between Blue Jays and gray squirrels for acorns
- Interspecies competition
  - For example, between hole-nesting birds for nesting sites, between sea birds for nesting rocks, or between birds in use of some food resources
- Intraspecies competition
  - For example, contests over territory, intolerance at feeding stations, feeding upon the same food sources, or using the same cover

Some animal ecologists have borrowed the term "coaction" from classical plant ecology; coaction thus used has as its principal phases *competition*, *cooperation*, and "*disoperation*." *

Minimum Area and Minimum Numbers. Variations in the territorial area held by birds indicate rather clearly that a minimum size exists below which the birds fail to breed successfully. In addition to the minimum size of *contiguous* territories, there exists also a minimum size of *isolated* habitat that will be used by species. For the purpose of this principle of minimum area, isolated habitat will be considered as any habitat separated from others of its kind. An island may be isolated by the water around it or a forested butte by the surrounding desert or grassland. Yet equally isolated from the ecological standpoint may be a glade in the forest, a clump of white pines in the hardwoods, or a brush patch in farm fields.

Minimum area and bird mobility are so interlinked that the daily cruising distance forms one of the limits to minimum area. But the better habitats have a rather lower minimum than poor ones. It may be presumed that where habitat is of choice quality, the bare minimum of area and cruising distance will have a chance to come into play. It has been said that the minimum isolated woodlot holding Ruffed Grouse is about 40 acres. An isolated quarter-acre marsh seems too small for the Song Sparrow and a woods of fewer than 5 acres too small for the Black-capped Chickadee.

The absence of some birds from isolated habitats, particularly birds of low mobility, has been explained as possibly resulting from a "clean sweep" by local misfortune for the birds present. With no surrounding population to restock the area, permanent depopulation occurs (Leopold, 1933). Influx from nearby reservoirs repopulates an area, rapidly for mobile species, slowly for others.

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* But a naturalist-philosopher expresses it better when he writes, "Nature red in tooth and claw—that is, competitive, or nature at peace—that is, cooperative; or nature in alternating moods, or at one and the same time, competitive and cooperative (her normal condition), is only in rare instances in balance for any extended period" (Bedichek, 1950).

The limit in numbers below which a species may not go and recover has been termed the *extinction threshold*. This minimum seems to have been reached by the ill-fated Heath Hen when the number dropped to about 200. A million birds may have been the extinction threshold for the Passenger Pigeon. For birds like the Starling introduced into the United States, the limit is low, for only a handful survived release to populate North America (see Figs. 10·11, 14·5).

The influence of minimum numbers (when compared to known limitations of excess numbers) testifies to a principle of optimum numbers, which can be stated simply as, "populations are most successful when in optimum numbers." The Passenger Pigeon nested in great concentration as well as in scattered groups; the latter were said to be less successful than the large ones. Large colonies of Herring and Lesser Black-backed Gulls show earlier laying, more uniformity, and greater success than others (Darling, 1938). Small colonies of Gulls, Terns, Gannets, and Fulmars have less success than large ones. A large colony of Yellow-headed Blackbirds has been reported to have a hatching success of 75.7 per cent in contrast to 60.6 per cent for a smaller one (Fautin, 1941). But few differences in success between large and small colonies of most species have been reported. A contribution to understanding the reasons for this difference in success appears in banding records for the Common Tern colonies of Cape Cod; these records evidence the importance of *longevity*, *site tenacity*, and *group adherence* (Austin, 1945, 1949).

DENSITY AND CHANGE

Population Densities. *Density* carries with it the thought of bird numbers in terms of space (usually area) though in a stratified environment, such as a forest, it may be suitable to consider volume (page 208). It can hardly be doubted that competition influences densities; yet in the year-around view, it can be assumed that basically the most important influence and determinant of bird numbers is the amount of food and cover present. It seems logical, though this has not been demonstrated as yet except in studies of a few gallinaceous game birds, that birds fill the environment to its capacity for them, the latter measured as carrying capacity (page 211).

The density of bird population varies widely geographically and ecologically; the total bird population varies as well as that of the species. Any bird student who has passed through a succession of cover types at any season is aware of differences in abundance of birds, both the total population and that of the various species. Table 14·2 shows some examples of comparative densities of birds in various habitats. The total species varied from twenty-one to forty-one and the density from 149 to 343 pairs per 100 acres. Table 14·2 also gives some parallel examples of comparative densities of the same species in the several habitats.

Table 14·2
Variation of Species Density in Various Habitats
(Data from Audubon Breeding Bird Censuses in 1942)

Species	Oak-Hickory (Ohio)	Oak-Maple (Illinois)	White Pine-Hemlock (Vermont)	Lowland Beech-Maple (Ohio)	Climax Beech-Maple (Ohio)
Downy Woodpecker	1	5	2	3	2
Red-eyed Vireo	5	14	4	2	2
Wood Thrush	2	2		3	2
Tufted Titmouse	2	2		2	3
Crested Flycatcher	1	8		4	2
Song Sparrow	2	1			
ALL SPECIES	34	21	41	24	25
Density (pairs per 100 acres)	149	223	225	215	343

In a study of winter birds of upland plant communities in North Carolina (Quay, 1947), the birds-per-acre densities were (November 1, 1939 to March 1, 1940) as shown in Table 14·3. Similar variations, either by ecological stages, as in the table, or by other cover types, are found on every hand, irrespective of the methods of determination used.

Mixed Densities. Because all birds must live from the same biological energy resources, competition among them tends to adjust their respective densities. But if no overlap of their life needs occurs, the densities of the various species in a habitat are independent of each other. The Blue-headed Vireo feeding and nesting in the upper story of the forest has no overlap with the Ruffed Grouse on the forest floor; their respective densities vary independently of each other. But some overlap occurs, for example, in the feeding habits of Vireos and Warblers. When food becomes scarce, this may influence their respective numbers. Various Shorebirds feeding along the beach compete with each other whenever the same food attracts them. In the same way, birds that use the same space are competitive. The Mountain Bluebird and Violet-green Swallow, both of which nest in holes, compete with each other for nesting sites.

Table 14·3
Abundance Rank of Species by Ecological Stages
(Total species reported, 42; average birds-per-acre, 4.35)

Species (part only)	Bare Field	Crab-grass	Crab-grass–Tall Weeds	Tall Weeds–Broom Sedge	Broom Sedge–Pine	Pine	Deciduous Woods	Pastures
Meadowlark	5	3		1				5
Killdeer	3							1
Mourning Dove	3					1		
Savannah Sparrow	2	5	3	3	3			2
Field Sparrow		1	5	5	5			
Slate-colored Junco	1	1	4	4	4	2	2	
Song Sparrow		1	3	3	3			
ALL SPECIES:								
Number	15	8	7	9	7	25	23	12
Average birds per acre	2.4	10.5		8.0	6.5	7.0	1.0	2.8

Source: Thomas L. Quay, "Winter Birds of Upland Plant Communities," *Auk,* 64(1947):382–388.

The net result of any joint use of habitat or any of its attributes is a *compensatory adjustment* of numbers. *Mixed density* actually means the density thus adjusted; it is not the same as the *combined density* of birds separate from each other or so interspersed through the habitat as not to influence the density of each other. It follows from this that the mixed density of two or more species is the sum of their normal, separate densities minus the proportion of overlap. Two species completely overlapping would have a mixed density identical with that of either alone. But if the overlap were 50 per cent, the mixed density would be of the order of three-fourths the combined density.

While this discussion of mixed density stresses competition in the use of habitat, some "cooperation" may be taking place unseen. If the Blue-headed Vireo protects the tree against insect attack, there may be more buds available to the Ruffed Grouse next winter. That being the case, the mixed density will be higher than the sum of the respective densities otherwise would be. Of this subject we know little.

Biomass. Studies indicate that for many purposes at least, populations should be considered on a *mass* rather than on a *numerical* basis. The total mass of animals measured by weight is termed the *biomass*, a most convenient term for the concept. Thus the number of Hairy and Downy Woodpeckers in a forest may be the same, but because the former is nearly three times the size of the latter (72 *vs.* 27 grams), its population has nearly three times the biomass, though the numbers are equal (Fig. 10·14). The habitat must support the birds, and our thinking is sounder when using size relations, for the biomass measures the avian tissue living off the energy resources of the land. Yet in all this, we must not overlook the fact that variations in biological efficiency may interpose difficulties as yet unmeasurable in our understanding of the biomass. It will be developed later in the section on food habits (Chapter 23) that birds vary in the amount of food needed. It has been shown also that the environment can support more biomass when organisms are in larger units than when in smaller ones.

The famed flock of Passenger Pigeons estimated by Alexander Wilson to total 2,230,272,000 birds and to require 17,424,000 bushels of mast daily had a Pigeon biomass (340 grams a bird) of perhaps 800,000 tons, which required about one-half million tons of mast daily (7½ ounces for each bird). Since fresh tree fruits like the acorn have about 54 calories per ounce (191 per 100 grams) of edible portion (about two-thirds of the acorn is edible), the daily consumption by the Pigeons thus estimated results in 360 calories per pound of bird. The Mourning Dove eats about 11 grams of grainaceous foods daily that average about 3.6 calories per gram. This would indicate a daily need for 39.6 calories, or about 180 calories per pound of Dove. The demands of avian biomass upon the habitat are indeed great, but the estimate by Alexander Wilson may have been twice as high as actually the case for sustained daily consumption. (A "feast and famine" type of eating in the wild, however, is a very real thing.)

The data of Table 14·2 have been converted, by using the probable average weights of the respective breeding birds, into biomass calculations of grams per 100 acres of habitat for the several cover types given in Table 14·4.

Table 14•4

Data of Table 14•2 Expressed as Biomass

Cover Type	Biomass (Grams)
Oak-hickory	4,404
Oak-maple	4,644
Climax beech-maple	5,891
Lowland beech-maple	7,023
White pine-hemlock	8,347

In the oak-maple type, some 6,800 additional grams of biomass belonged to species feeding off the area. These uncounted birds (like Cowbirds and other visitors) must be kept in mind. The conversion shows differences that we may interpret roughly as *support differences* in the several habitats. The *biomass-density* thus becomes a useful tool in population studies. Additional biomass data would be useful in furthering comparison. No doubt also, internal biomass comparisons, as of predator and prey, would prove useful. The total or *habitat biomass* could include all animal life in addition to birds; it also could be of the plant life or of the animal and plant life combined.

Population Reservoirs. Because of the space needs of birds, whether territorial or not, males unable to find suitable or unoccupied habitats will be unable to obtain mates (Chapter 12). Conversely, females unable to find males occupying habitat for nesting will likewise go unmated. These two groups form a reservoir of unmated birds drawn upon to fill vacancies occurring among mated pairs. How large a reservoir exists is not known; indications are that it may become large, locally equalling the number of breeding birds.

The unmated birds form a floating population, evidently not engaging in great strife with mated pairs but being tolerated by them. Records indicate quick replacement of one member of a pair lost through tragedy. A male Bald Eagle of a nesting pair was collected by an ornithologist. Within a week, he had been replaced by another that defended the nest as actively as his predecessor. Experimental removal of one of a pair of mated birds has shown replacement by another bird (possibly in late afternoon though more likely in early morning), so that the final parental duties were carried out by foster parents several substitutions removed from the original, biological parents. That there are differences in the remating rate of various species seems likely; likely also are variations with region, season, and breeding cycle. Differences in sex ratio and age classes may influence the utility of the reservoir. All of these points need investigation; and a few such studies have been made (e.g., Stewart and Aldrich, 1951).

Population Cycles. The variations in bird numbers may conveniently be considered as of an *irregular, cyclic,* or *secular* nature. Changes in the density of bird life resulting from environmental variation may be any one of the three, though our knowledge may not always permit a high degree of accuracy in determining which one. A change of bird life in the wake of a hurricane would be considered as an irregular or random one, that occurring from a climatic cycle would be a cyclic one, and one in accordance with plant succession would be a secular one.

The number and variety of nonrhythmic fluctuations are almost unlimited, but rhythmic (periodic) ones are more limited in scope. Cycles of population abundance appear to be rather common, though very few have been analyzed. A long record of population usually shows cyclic fluctuation (perhaps always), random fluctuations, and a trend. The combined cyclic elements in such a record is termed

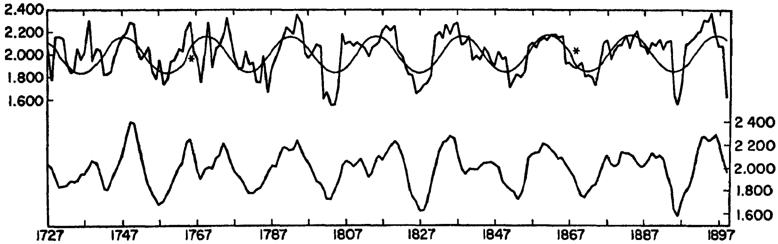

Fig. 14•4. *The logarithms of the European Partridge at Krumau as shown by game-bag records has a manifest cycle of about 23 years. This is composed of many periodicities of which the strongest cycle measures 22.71 years. Irregular fluctuations and a trend are present also, but the latter has been neutralized by use of a 23-year moving average. The lower curve consists of seven cycles derived from the Partridge record: 22.71, 13.95, 11.84, 8.33, 8.05, 5.09, and 4.14 years. The shape and timing of these seven together will repeat identically only once in about five million years. (After Leonard W. Wing, "Cycles of European Partridge Abundance,"* Journal of Cycle Research, *2(1953):56–76.)*

a *manifest cycle* to distinguish it from the periodicities of which it may be formed or which may be derived from it. Fig. 14·4 shows a manifest cycle of abundance that proves to be composed of many periodicities, along with both random fluctuations and a trend. The intervals between highs and lows of such a manifest cycle may vary by several years, yet be composed of fixed cyclic elements that have become manifest in many cases for scores of years.

The most common variations, both cyclic and noncyclic, are those of population number from year to year. One of the events involving both abundance and movement is the flight of northern birds, such as of the Snowy Owl which appears to follow a manifest cycle of about 4 years in length. Population changes of the Ruffed Grouse have a manifest cycle commonly known as a "ten-year cycle." It is likely that any attribute environmentally related should be considered subject to environmental fluctuation. In addition, internally controlled factors may show rhythms as an inherent trait of a biological system.

Exotics in a New Environment. Two opposing views maintain respectively (1) that exotics cannot become established unless a vacant niche exists and (2) that a vigorous exotic species will carve out a niche for itself. It seems probable on theoretical grounds that no bird can survive in an alien climax. All exotics (at least so far as reliably known) established in strange lands are birds becoming established in settled areas (therefore disturbed) rather than in climax habitats; this fact supports the first view.

The famed *sigmoid population curve* is used little in field ornithology except in the study of exotics in new environment, expansion of resident birds under changed conditions, or population recovery from local misfortune. The sigmoid (s-shaped) curve reflects the characteristic of a population to expand slowly at first, then to rise rapidly, and finally to taper off at a new level (Fig. 14·5).

All Starlings in America are quite likely descended from the 160 birds (eighty pairs at most) liberated in New York City in 1890 and 1891. The pioneer front appeared in an area first as winter stragglers mostly and perhaps always as young birds; establishment as a breeding bird followed after about 5 years or so. The Starling spread somewhat more slowly than did the House Sparrow (Wing, 1943a). The Starling took more than 60 years to cover suitable area that the Sparrow overran within about 40 years of its introduction. The Starling migrates in America in a northeast to southwest direction. Its highest density extends as a belt from the Middle Atlantic states to about Central Texas. Washington, D. C., near one end and San Antonio near the other are both well known for the undesirable habits of Starlings. The Starling has also been introduced elsewhere and has

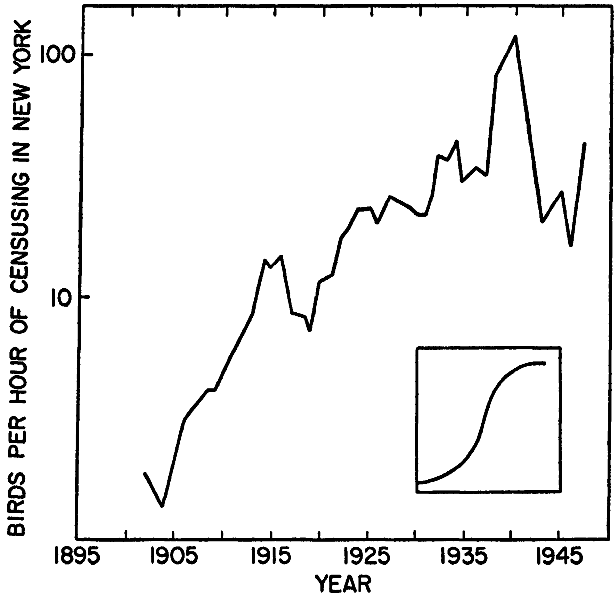

Fig. 14·5. *The number of Starlings reported in the Christmas censuses per hour of censusing smoothed by moving averages of three and plotted on semilogarithm paper. Inset: The general shape of the sigmoid curve of population. (After David E. Davis, "The Growth of Starling,* Sturnus vulgaris, *Populations,"* Auk, *67(1950):460–465.)*

thrived. It is the most widespread of thirteen European birds introduced into Australia and New Zealand (Williams, 1953).

The British Goldfinch on Long Island, Mute Swan in the New York region and Oregon coast, European Tree Sparrow near St. Louis, Chinese Spotted Dove in Los Angeles, and Mynah in British Columbia have become established locally. Game birds introduced have been the Ring-necked, Chinese, and Mongolian Pheasants, the European Partridge, and the Chuckar Partridge. Native American birds which have been moved and therefore are exotic in some areas are the House Finch, Bob-white, Valley Quail, probably the Mountain Quail, and perhaps the Prairie Chicken.

BIRD NUMBERS

Relative Abundance of Species. Our information on bird population does not permit us to list relative abundance of species with complete confidence. If we may judge by the Christmas censuses, the most frequently reported and perhaps most abundant winter birds in eastern America are:

American Crow
Red-winged Blackbird
Starling
American Robin
Slate-colored Junco
Tree Sparrow
Cardinal
Grackle (Bronzed and Purple)
Cedar Waxwing
White-breasted Nuthatch
Horned Lark
Downy Woodpecker
House Sparrow
Cowbird
American Goldfinch
Black-capped Chickadee
Blue Jay
Song Sparrow
Golden-crowned Kinglet
Tufted Titmouse
Mockingbird
Eastern Bluebird
Eastern Meadowlark
Mourning Dove

Our knowledge of bird abundance in summer does not give us the same assurance. The most abundant or most frequent ones over much of eastern North America seem to include:

Song Sparrow
Chipping Sparrow
American Robin
Mockingbird
Red-winged Blackbird
Eastern Meadowlark
House Sparrow
Cowbird
Vesper Sparrow
Yellow Warbler
Barn Swallow
Mourning Dove

Total Populations. Just how many individuals of the various species or subspecies there may be is certainly an important objective for bird study to attain. Some indication of the bewildering variation in numbers of birds may be had from Table 14·5.

Table 14·5

Some Estimated Numbers for Several Species of Birds

Species	Number
Whooping Crane	16–35
Ross Goose	6,000
Greater Snow Goose	25,000
Laysan Teal	50
White-tailed Ptarmigan	100,000
Franklin Grouse	100,000
White-winged Dove	5,000,000
St. Kilda Wren	136
Golden-cheeked Warbler	1,000
Kirtland Warbler	1,000
House Sparrow (America)	150,000,000
Harris Sparrow	8,000,000

Changes with Time. Important information has been obtained by observers that shows secular changes in bird populations, changes both for more and for fewer birds. On San Martin Island off the coast of Baja California, about thirty pairs of Ospreys nested in 1913; the population of 1946 consisted of only three pairs. Man is considered the most important enemy. The Common Redpoll has been rare in Ohio during the twentieth century, though often found there earlier; but Cardinals are more numerous than previously (Moseley, 1946).

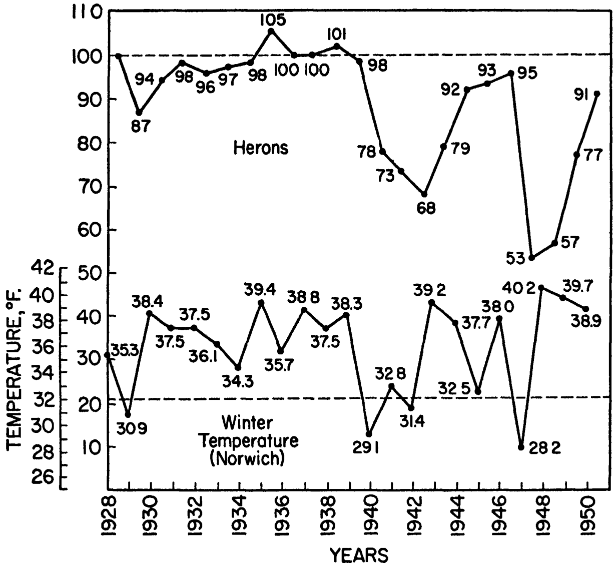

Fig. 14·6. *Index of British Herons (1928, 1936, 1937, 1938, and 1939 number of nests equals 100) compared to winter temperature. (After W. B. Alexander, "The Index of Heron Population, 1950,"* British Birds, *43(1950):78–80.)*

Avocational British ornithologists have shown great zeal in obtaining an index (number of nests for 1928, 1936, 1937, 1938, and 1939 taken as 100) of year-to-year Heron numbers. This shows that a most important influence is winter temperature. After an unusually cold winter, as that of 1946–47, recovery of normal numbers requires 2 to 4 years (Fig. 14·6).

A study of interest records the growth of a Caspian Tern colony in the San Francisco Bay region from 1922 to 1931 (Miller, 1943). The yearly count from 1922 to 1931 is given in Table 14·6 (after a lapse of 12 years in the count, 378 nests were found in 1943). A 5-year census of a virgin Palouse Prairie (Wing, 1949) showed a

Table 14·6
Caspian Tern Count of a San Francisco Bay Colony

Year	Number of Birds	Year	Number of Birds
1922	7	1927	212
1923	2	1928	242
1924	12	1929	–
1925 (estimate)	35–50	1930	296
1926	164	1931	287

Source: Alden H. Miller, "Census of a Colony of Caspian Terns," *Condor*, 45(1943):220–225.

relative uniformity of total numbers per hundred acres, though some intercompensatory adjustments occurred (Table 14·7). Counts of Common and Roseate Terns on Weepecket Island, Massachusetts, varied between 2,000 and 4,000 from 1896 to 1940. They were displaced by Herring Gulls, which varied in number from four in 1935 to 1,000 in 1943 (Crowell and Crowell, 1946). Actually, examples of changes in bird life may be found throughout the world; some may be attributed to man but others may not (Fig. 14·7).

Table 14·7
Breeding Bird Censuses on a Virgin Palouse Prairie

Year	Number of Birds
1942	248
1944	227
1945	258
1946	248
1947	248
Average	246

Source: Leonard W. Wing, "Breeding Birds of Virgin Palouse Prairie," *Auk*, 66(1949):38–41.

Total Number of Birds. Because we have no data on the bird population of America in pre-Columbian times, our conclusions on changes with settlement must be based largely on knowledge of circumstances. As mentioned elsewhere, some birds have declined in numbers, some have increased. But because the climax appears to be the most efficient energy stage (page 199), it seems likely that it in turn supports a higher population of birds, at least on a biomass basis, than other ecological stages. Censuses of birds in climax and nonclimax environments support this assumption, though the many vari-

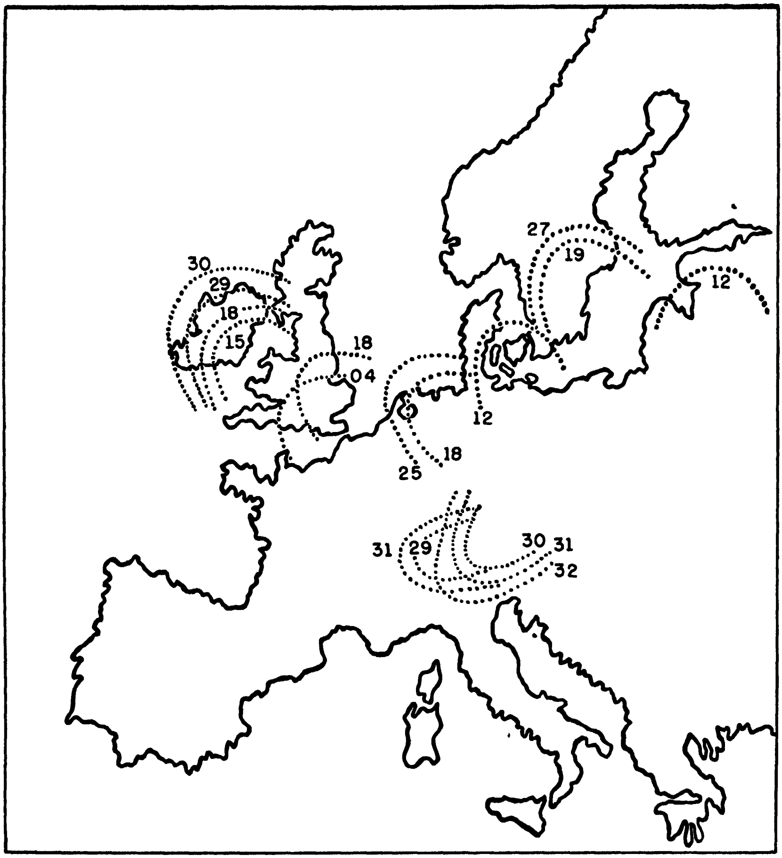

Fig. 14•7. *Invasions of the Black-necked Grebe into Europe in the twentieth century are thought to be associated with drought conditions in the dry lands of Central Asia. (After Olavi Kalela, "Changes in Geographic Ranges in the Avifauna of Northern and Central Europe in Relation to Recent Changes in Climate,"* Bird-Banding, *20(1949):70–103.)*

ables involved make comparative evaluation difficult. On theoretical grounds at least, it seems entirely probable that compared to 1492 both fewer birds and a smaller avian biomass exist today in North America.

The total number of birds today may be estimated for a few areas on the basis of census reports, such as the Christmas censuses or breeding bird censuses of the United States and Canada. In addition, sample censuses reported by various observers add to our information. Several attempts have been made to form a suggestive estimate, and no doubt more and improved ones will be forthcoming from time to time. On the basis of our present knowledge, the breeding populations of the United States seem to be about 5.6 billion birds. A comparison between appropriate climax and nonclimax areas indicates that the former runs substantially higher in bird life, sometimes more than 25 per cent greater. This would perhaps permit us the assumption that the bird life under pristine conditions totaled proportionately more. On the basis of kinds of area in the much smaller space of Great Britain, hence one where studies are far easier and the problem less complex, the bird population is estimated at about 120 millions (Fisher, 1940). The world's bird life may in turn total one hundred billion.

SUGGESTED READING

ALLEE, W. C., ALFRED E. EMERSON, ORLANDO PARK, THOMAS PARK, and KARL P. SCHMIDT, *Principles of Animal Ecology*. Philadelphia: W. B. Saunders Co., 1949.

CLEMENTS, F. C., and VICTOR SHELFORD, *Bio-ecology*. New York: John Wiley & Sons, Inc., 1939.

ERRINGTON, PAUL L., "On the Analysis of Productivity in Populations of Higher Vertebrates," *Journal of Wildlife Management*, 6(1942):165–181.

ERRINGTON, PAUL L., "Predation and Vertebrate Populations," *Quarterly Review of Biology*, 21(1946):144–177, 221–245.

KENDEIGH, S. CHARLES, *Measurement of Bird Populations*. Ecological Monographs, 14(1944):67–106.

KLUIJER, H. N., "The Population Ecology of the Great Tit," *Ardea*, 39(1951):1–135.

*LEOPOLD, ALDO, Game Management. New York: Charles Scribner's Sons, 1933.

LOTKA, ALFRED J., *Elements of Physical Biology*. Baltimore: Williams & Wilkins Co., 1923.

PEARL, RAYMOND, *The Natural History of Populations*. New York: Oxford University Press, 1939.

PEARSE, A. S., *Animal Ecology*. New York: McGraw-Hill Book Co., Inc., 1939.

SIMPSON, GEORGE GAYLORD, and ANNE ROE, *Quantitative Zoology*. New York: McGraw-Hill Book Co., Inc., 1939.

*WING, LEONARD W., *Practice of Wildlife Conservation*. New York: John Wiley & Sons, Inc., 1951.

15

Bird Flight

As a means of moving under low power, swimming has advantages over land and air travel. The ease with which a man can push a water-borne burden or the low horsepower per ton that moves a loaded boat illustrates these advantages as compared to land or air travel. Additionally, the animal does not have to use energy for carrying the body or maintaining posture; the water supports the weight. But water travel is a slow-speed proposition. Increase of speed in water means a very great increase in resistance. It also confines the water animal to water areas. The ability to travel on land, however, opened new horizons to the ancestral land animals previously confined to the sea. It also opened opportunities for a little more speed and mobility, though this increase was probably not very great.

In like manner, moving a burden by air is more costly in consumption of energy than moving it by land or sea. The bird in flight must carry the weight by support generated with muscle rather than resting it on the ground or supporting it in the water. But greater speed is possible and especially so is greater mobility; the flying bird moves into a realm having few occupants. The cost in efficiency is a rather small price to pay for the great advantages offered by flight.

The ability to fly and all the many advantages that consequent mobility and speed confer upon its possessors dominate the life of the bird. Even though we can study the facts of flight, many of which have been clarified by man's learning to use mechanical flight, our knowledge of its origin must be largely conjectural, but knowledge of the facts of flight does make conjecture intelligent.

THE ORIGIN OF FLIGHT

Four or five theories have been advanced to explain the origin of flight; several additional ones concern its early development (as dis-

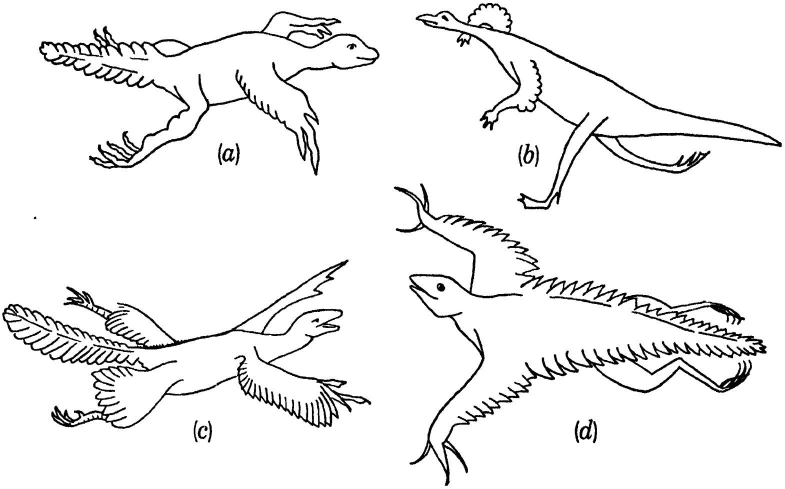

Fig. 15·1. *Drawings to illustrate some theories of the origin of flight: (a) Arboreal animal with flight feathers developing on limbs and tail. (b) Cursorial animal with feathers developing on forelimbs for beating the air. (c) Four-winged stage of gliding arboreal animal. (d) Arboreal animal with feathers developing on forelimbs, side, and tail for gliding.*

tinguished from its origin). The theories of origin rest upon certain facts. The flight of birds, for example, involves the forelimbs, with no primary adaptations of the hindlimbs for flight. The motive power has been transferred from the forelimbs to the body (pectoral) muscles. No living or fossil bird shows development of any flight devices other than forearm wings (except possibly the postulated four-winged stage), and most (if not all) structures associated with flight are but modifications of standard vertebrate possessions. Bird flight, be it noted, makes effective use of the various known principles of aerodynamics.

Cursorial Origin. The cursorial theory (Nopsca, 1907, 1923) holds that birds arose from a running ancestor that sped over the ground on its hindlimbs, its forelimbs flailing the air to aid balance. The theory proposes further that growth of scales which flattened into feathers aided their wearer in increasing its stride into a series of leaps lengthened by the flapping of these "feathered" forearms. In time, this developed into flight (Fig. 15·1). "Water-walking" may perhaps have been somewhat similar (Erickson, 1955).

Arboreal Origin. The arboreal theory has the flying bird descended from an ancestor that climbed trees to live an arboreal life (though the arboreal ancestor itself may have evolved from a ground ancestor). The claws and fingers on the wings of *Archaeopteryx* combined with two wings having weak musculature suggest to the proponents of the arboreal theory a soaring or gliding animal. Thus, the animal climbed about in the trees and glided or volplaned to another necessarily lower position, somewhat as do the flying squirrel and flying lemur of today (Fig. 15·1).

The discovery of apparent vestiges of quill feathers on the thighs of a number of embryos (and possibly upon adults also) as well as upon *Archaeopteryx* has given rise to the postulate that an early stage in flight involved planelike feathered structures on both the fore- and the hindlimbs to give a four-winged condition (Beebe, 1915). The forelimbs dominated so that the four-winged condition went out of style (Fig. 15·1).

Combination Theory. The ideas of arboreal and cursorial origins have been combined into one holding that the pro-aves animals both ran on the ground and ascended trees, where they perched upright on limbs. The hindlimbs were somewhat like those of birds of today and bipedal dinosaurs of yore. The three fingers were for climbing, and the animals hopped lightly from limb to limb, partially supported in transit by folds of skin at the joints of arms and legs. Later, long scale-feathers developed on the forelimbs, hindlimbs, and tail. Flapping the forelimbs bearing these scale-feathers provided an advantage which in time gave rise to wings.

Diving Origin. On the assumption that water birds are the most primitive birds today and arboreal ones the most specialized, the diving-origin theory suggests that flight arose from gliding or soaring out over the water for fish, the pro-aves starting from a cliff or elevated perch and swimming back to land. The strong-flying sea birds arose thus from these ancestors and the land birds from sea birds. While this has been proposed as an additional theory, it really does little except to substitute cliffs for trees in the arboreal theory.

Wind-Response Origin. Organisms meet the problem of wind in the environment by passiveness on the one hand (as by loss of flight or by hiding low in the grass) and by aggressiveness on the other (as by greater flight powers or by strong climbing). In aggressively meeting the wind, the wind-response theory proposes that the pro-aves animal developed tendencies to let wind carry some weight; the strength thus released was used for locomotion on the ground; penetration of the trees and water came later. The forelimbs did not decline in vigor to reverse their evolution later in becoming wings, as bipedal theories usually must assume.

FLIGHT IN OTHER VERTEBRATES

Fishes. Fishes of several families in warm marine waters (and a few of tropical fresh water) have developed aerial locomotion of sorts. But none uses its "wings" (actually enlarged pectoral fins) to flap or otherwise to propel itself through the air. Some members of the family Cypseluridae (perhaps all) "fly" by unfolding the pectoral fins and gliding stiff finned. They swim at high speed immediately under the surface, rise to the surface, spread out their fins and taxi along, propelled by vigorous side-to-side motions of the especially powered tail, almost always into the wind (Schultz and Stern, 1948). If sufficient *lift* is generated, the fish may leave the water entirely for from 2 to 20 seconds and for 10 to 60 feet after a run of about the same length in the water (Fig. 15·2). Flights lasting more than half a minute and reaching more than 30 feet above the water and 1,000 feet long have been reported. The speed of taxiing and flight may reach 20 to 40 miles an hour. It should be noted that this differs from true flight in that true flight always receives its generating or continuing force in the air.

Amphibians. The flying frog (*Polypedates*) of the East Indies makes a slanting glide, reported to total not more than 30 to 40 feet, from an elevated position. These frogs have large webbings stretched between the toes of all feet (Fig. 15·3).

Reptiles. Pterosaurs, often called "flying dragons," have been the reptilian bid to dominate the air (Fig. 15·3), though none survived the Mesozoic era. It seems reasonably clear that the pterosaurs descended from thecodonts. Presumably, they had a batlike locomotion; perhaps they also clung to objects like bats.

The fifth (commonly called "little finger") of pterosaurs grew long and strong to stretch a membrane for flight (see Fig. 1·14). The remaining fingers remained small, though still clawed. If we may judge by the bones for attachment of flight muscles, the larger pterosaurs had a weak flight at best, possibly a soaring or Vulture-like flight. The smaller pterosaurs may have been somewhat batlike in flight.

Flying reptiles varied in size but were comparable to modern birds. The largest (*Pteranodon*) owned a 25-foot wing spread, the greatest of any animal living or dead. Perhaps it soared and occupied a niche in the Mesozoic community somewhat as Vultures do today; we may assume safely that fleshy animals died and provided food for any Vulturine pterosaur. The horny beak of *Pteranodon* and the weak teeth of *Rhamphorhyncus* suggest the habit of feeding upon inactive

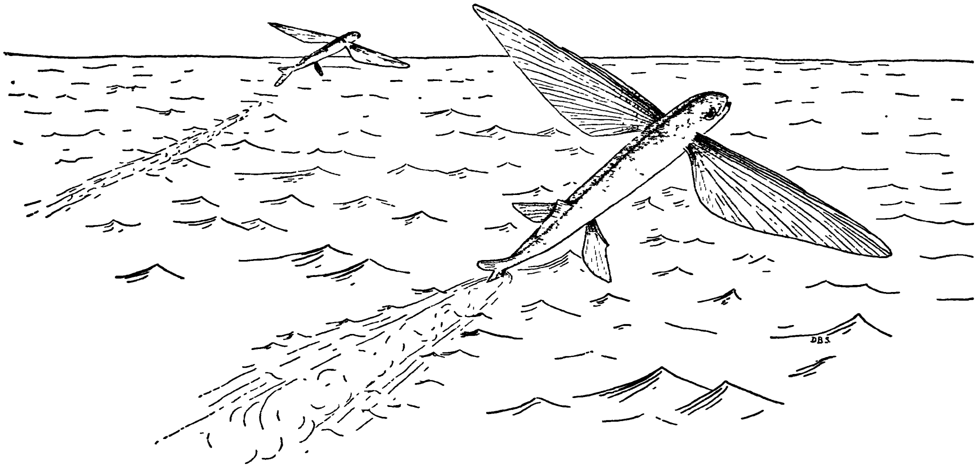

Fig. 15·2. *The flight of* Cypselurus, *a flying fish of the tropical Pacific waters. (By permission from* The Ways of Fishes, *by Leonard P. Schultz and Edith M. Stern p. 20. Copyright, 1948, D. Van Nostrand Co., Inc., New York.)*

food. But one can hardly postulate a use for the great bony crest on the head of *Pteranodon* (Fig. 15·3).

A small, living lizard (*Draco volans*) of southeastern Asia and adjoining islands has a thin membranous skin over extended ribs to form a gliding surface. The lizard can glide from a high to a lower position. Writers sometimes called it a "flying dragon."

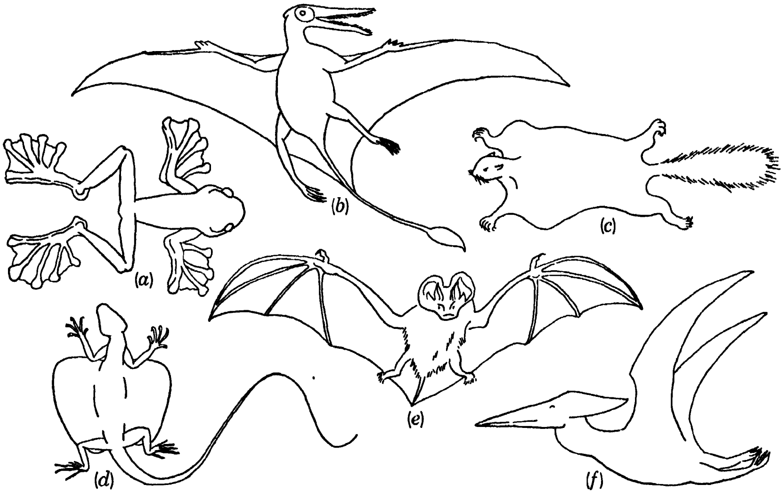

Fig. 15·3. *Flight in the vertebrate world other than in birds.* (*a*) *"Flying Frog,"* (*b*) *Pterodactyl,* (*c*) *Flying Squirrel,* (*d*) *"Flying Lizard,"* (*e*) *Bat,* (*f*) *Pteranodon.*

Mammals. The only mammals to develop the power of flight belong to a single order, Chiroptera (Fig. 15·3). Flying squirrels and flying lemurs actually glide from a high to a low elevation by a peculiar looseness of the body skin (Fig. 15·3). All bats fly by means of a membrane stretched between the fore- and hindlimbs, sometimes also including the tail (see Fig. 1·14). The elongated fingers of the bats support the membrane, but it is the third or middle finger that is elongated most; the first (thumb) remains free. The flight muscles of bats have considerable power and in consequence the breast bone possesses a well-defined keel, an evolutionary parallel of the bird.

Bats lack the aerial powers of birds, however, which fact results from several less advantageous characteristics. The feathers of the bird shape the wing to make a highly efficient *airfoil* (Fig. 15·4). The structure of the feather makes possible such characters also as "slots," "flaps," "propellers," and the like, in accord with sound aerodynamic principles. The bird has become modified far more for an aerial life; the bat itself differs little anatomically from a land mammal except for wings. Its flight muscles average about 7 per cent of the body weight in comparison with the average of 17 per cent for the bird (Hankin, 1913). In addition, the bird has a superior streamlined body shape. Bats with their supersonic detection device have a very great, specialized adaptation for a particular type of night hunting for insects.

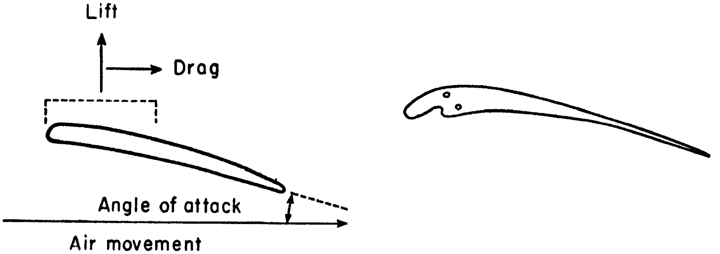

Fig. 15•4. Left. *Relationship of lift and drag to an airfoil at a moderate angle of attack. The major lift occurs in the part of the wing marked by the dotted line.* Right. *The airfoil of a Vulture* (Otogyps calvus). *Air passing over the top of the wing must travel faster than that passing across the lower surface. Hence, the air pressure is lower on the top so that the wing exerts* lift. *This is in accord with Bernoulli's theorem (as applied to unconfined gases).*

But cruising does not seem so efficient a use of energy in hunting insects as does the method of the Kingbird, for example, which stays at rest and thereby saves energy until insects come by. Yet the bat can utilize a food source otherwise largely unexploited by the vertebrate world. Its night life follows the tendency of small mammals to be nocturnal, an uncommon tendency among birds.

AERODYNAMICS OF FLIGHT

Flight Structure. The advent of the airplane has clarified many points about bird flight while obscuring others (though no aerodynamic principle used by airplanes appears to be unused by birds). Body modifications have been described (Chapters 3, 4, 5), though they are so many and so varied that they cannot be given justice in a treatment covering much less than a whole volume in itself. The fundamental structures of flight are (1) the skeleton that forms the framework, (2) the muscles that propel the wings, (3) the nervous tissue that coordinates action, (4) and the feathers that meet the air stream.

The skeletal parts are rigid in construction and light in weight. The Frigate or Man-o'-war Bird, for example, weighs about 32 ounces and has a wing spread of 7 feet; yet its bones are said to weigh about 4 ounces. Some other skeletal and body weights are given in Table 15·1. The shoulder joint has relatively great freedom of movement. The elbow moves forward and backward only; its rigid construction precludes up and down motion. The hand has considerable movement at the wrist joint but little otherwise except for the opening and closing action of the *alula*. The wrist joint retains sufficient flexibility to open, spread, and rotate for advantageously opposing air currents.

Table 15·1
Body and Skeletal Weights

Species	Body Weight (Grams)	Skeletal Weight (Grams)
Canada Goose	4,500	249
Blue-winged Teal	330	18.1
Golden Eagle	4,750	230
Screech Owl	160	4.9
Barred Owl	900	61
American Robin	80	3.2
Cardinal	38	2.0

The primaries, but especially the secondaries and sometimes tertiaries, serve as the supporting surface opposed to the air. The warm air in the body and feathers decreases specific gravity slightly. The wing coverts function in flight almost entirely to shape the wing in forming an airfoil of efficient design (Fig. 15·4). (*Airfoil* is a term of aerodynamics meaning the shape of a cross-section of the wing; though in England and sometimes elsewhere, it may also be used interchangeably with *wing*.) They serve also to give a smooth surface having low friction with air. Because all feathers overlap each other, a rather solid, airtight structure results.

While all surfaces may serve to supply *lift*, it comes chiefly from the inner wing (secondaries and tertiaries), primaries, and tail, in that order. From time to time, it may be noted, relative lift by the supporting structures may vary somewhat from the usual condition. The primaries are said to function principally as producers of forward motion, similar in this respect to the propeller of an airplane. But this interpretation has been questioned by aerophysicists. The alula functions as an air slot to increase lift; it may possibly serve additionally as a "paravane" in diving birds. The tail serves as an extra planing surface, though at times it may act as a slot, flap, rudder, elevator, or brake.

Properties of Air. Air, like other gases, varies in density with temperature and composition. Dry air at standard conditions (32° F. at 29.92 inches of barometric pressure) weighs about 0.081 pounds per cubic foot. Pressure and temperature of air change with altitude, as any mountain visitor can testify. (For ordinary field work, we may consider that temperature drops about 3° F. for each 1,000 feet rise in altitude.) Birds live only in the lower atmosphere, even on mountain tops.

Because water vapor has a density but about five-eighths that of air, humidity lowers lift and increases the power needed. In the same way, the less dense air of high altitudes offers less lift. In consequence of lowered densities in humid atmospheres and high altitudes, some adjustment of wing loading occurs among birds adapted for high altitude and for humid regions.

Flight Mechanics. Air resists the efforts of a body to move through it; conversely, moving air has force. From the standpoint of an object, the force is the same whether the air moves and the object remains stationary or the object moves and the air remains motionless. Flight concerns itself with the *relative movement* of the air and object. Air flowing around a perfectly streamlined object would exert pressure equally on all sides. But transfer of force to the object will move it when the force exceeds the inertia or anchorage of the object. This is the plan of the wing (Fig. 15·4). The greatest reduction of pressure occurs at the top and especially at the leading edge where the wing first meets the passing air stream. Hence, the wing supports the bird. If the *angle of attack* becomes too great, the leading edge "stands in its own air-stream shadow." The streamline of air does not follow the air foil; lift is lost. To prevent stalling or to lower the stalling speed of the moving air-borne body, slots are used to deflect or to pass the air stream back along the upper wing surface. In a sense, the slot acts like a small airfoil ahead of the leading edge. The bird uses the alula to deflect the air current down to the wing at slow speeds with high attack angles. Slots may also be formed between the wing and body to smooth the air stream over the tail. It is probable also that the primaries may at times form air slots, particularly the outer ones with their greater flexibility and control. The trailing edge of the wing cannot be let down like an airplane flap to increase camber and lift at slow speeds, but the wing may be rotated to increase camber. The tail may be used as a "flap" also.

Because of nerve endings in the skin near their bases, nearly all feathers of the wing can act as sensory receptors. Practically every point of the wing may respond and thereby bring about continuous variations and adjustments up and down the wing, all of which make difficult the task of comparing bird wing action with that of a fixed, mechanical wing.

The primaries twist to take advantage of air conditions, reportedly somewhat as may a variable-pitch propeller in an airplane. The outermost primary with the superior control encumbent upon it is evidently the most important feather. Indeed, it is reported that a few species may be nearly or quite flightless if this primary is lost. But the concept of wing-tip propellers is a postulate probably not based upon sound facts.

The slight difference in pressure on the upper side of the wing exerts very great lifting force. An average difference over the wing surface (280–295 square inches) of a Barred Owl (weight 600–900 grams) amounting to but one-hundredth of a pound per square inch would give a total lifting power of nearly 3 pounds, which would carry the bird—even with a rat in its talons.

In general, lift and *drag* vary with square of the speed. The lift varies more or less proportionally to angle of attack and area of wing. Twice the wing area or twice the angle would carry twice the load but to double the speed would take eight times the power. Twice the *camber* (curvature), however, would about quadruple the drag.

The ratio of length to width of the wing is called the *aspect ratio*, and is large for soaring birds that live in the open and ride the air currents. Because tip vortexes cause reduction in efficiency for some distance inward, a long wing increases efficiency for flyers by increasing the proportion of inner, more efficient wing. For birds that need a very great power most of the time or that must operate in close quarters, the wide wing of small ratio gains more in usefulness than it loses in efficiency.

A moving body sometimes generates static electricity, which presumably occurs in birds also; at least it can be done experimentally with feathers. Whether the factor of static electricity influences the flying bird is not known.

Wing Loading. Birds tend to have variable wing loads (weight per unit of wing) in accordance with species and flight pattern. Soaring birds have low wing loads; fast flyers with rapid wing beat have larger ones. No doubt the additional bearing surface brought against the air when need be, such as the tail, enters into the loading. Measurements of the Barred Owl and Ruby-throated Hummingbird are given in Table 15·2.

Wing loadings, in pounds per square foot, without allowing for lift from the tail or for differences in lift between the secondaries and primaries, are given in Table 15·3. Wing loadings, it should be noted, do not take into account the length or efficiency of various wings.

The wing load in pounds per square foot of some soaring birds has been reported as (Hankin, 1913): Adjutant, 1.54; Cheel, 0.55; White Vulture, 0.87; Common Vulture 1.13; Old World Black Vulture (*Otogyps*), 1.23.

Table 15·2

Measurements of Barred Owl and Ruby-throated Hummingbird Expanse (Square Centimeters)

	Barred Owl (Sq. Cm.)	Ruby-throated Hummingbird (Sq. Cm.)
Wings	1,885	9.7
Head	143	1.3
Body	314	2.6
Tail	324	3.2
Total	2,666	16.8

Table 15·3

Wing Loading

Species	Weight (Grams)	Wing Area (Sq. Cm.)	Pounds per Square Foot	Grams per Thousand Square Centimeters
Black-capped Chickadee	12.5	76.0	0.3	164
Barn Swallow	17.0	118.5	0.3	143
Tree Swallow	20.1	125.0	0.3	161
House Sparrow	24.5	92.5	0.5	265
Leach Petrel	26.5	251.0	0.2	106
Purple Martin	43.0	185.5	0.5	232
Nighthawk	75.2	349.5	0.4	215
American Robin	82.0	244.0	0.7	336
American Sparrow Falcon	137.0	372.0	0.8	368
American Woodcock	198.5	354.7	1.1	560
Bob-white	198.6	216.8	1.9	916
American Crow	552	1,344	0.8	411
American Marsh Harrier	615	1,696	0.7	363
Peregrine Falcon (male)	712	1,146	1.2	621
Peregrine Falcon (female)	1,222	1,342	1.8	910
Mallard Duck (female)	1,234	952	2.6	1,295
Mallard Duck (male)	1,408	1,029	2.7	1,368
Osprey	1,798	3,211	1.1	560
Turkey Vulture	2,409	4,356	1.1	553
Golden Eagle	4,664	6,520	1.4	715
Whistling Swan	5,943	4,156	2.9	1,430

Source: Adapted from Earl L. Poole, "Relative Wing Weights of Bats and Birds," *Journal of Mammalogy*, 17(1936):412–443, and Earl L. Poole, "Weights and Wing Areas in North American Birds," *Auk*, 55(1938):511–517.

Maneuvering. Birds turn and twist in the air chiefly by changing the relative pressure against the respective wings. While all birds (including Swifts) beat their wings in unison, they can raise, lower, shorten, twist, and even stop one wing while the other continues to supply power. One wing can act as a brake to turn the bird. In some cases, the tail may be brought into play to serve as a rudder, but more often the tail is used to "trim" the flight.

Birds alighting upon a solid substance must stop their forward motion in time to prevent damage to their relatively weak legs and feet as well as to the body itself. This they accomplish by increasing the angle of attack, spreading the wings, spreading the tail downward like a flap, back paddling, and sometimes by elevating the body proper against the air stream.

Water birds do not need to use as much care in braking to a stop before alighting, because the water itself will cushion the impact somewhat. Some diving birds close their wings and plummet to the water, depending upon the force of their fall to carry them down. But others increase the angle of attack to a stall and go down by a tailspin-like plunge (page 440). Plungers may have the body cushioned for supplementing the protection afforded by the feathers (see Fig. 23·3).

Wing-Flapping Rate. The flapping rate depends upon flight style, size and shape of wing, motion rate of the wing pressure center, ground speed, and air motion (Blake, 1947). That it varies with the intention of the bird as well as with aerodynamics seems obvious, just as the stepping rate of a vigorous man depends upon where he is going—uphill, downhill, or wherever—and on how rough is the

Table 15·4
Wing-Flapping Rates

Species	Rate per Second	Species	Rate per Second
Double-crested Cormorant	2.6	Tree Swallow	3.5
Black Duck (?)	2.0	Bank Swallow	2.8
American Sparrow Falcon	2.4	Rough-winged Swallow	3.9
Ring-necked Pheasant	3.2	Barn Swallow	3.9
Killdeer	2.4	Cliff Swallow	3.9
Great Black-backed Gull	2.0	Purple Martin	4.4
Herring Gull	2.3	Blue Jay	2.6, 3.4
Laughing Gull	2.45	American Crow	2.0
Rock Dove	3.0	American Robin	2.3
Mourning Dove	2.45	Eastern Bluebird	3.1
Belted Kingfisher	2.4	Starling	3.3
Northern Flicker	2.2	Eastern Goldfinch	4.9

Source: Charles H. Blake, "Wing Flapping Rates of Birds," *Auk*, 64(1947):619–620, and Charles H. Blake, "The Flight of Swallows," *Auk*, 64(1948):54–62.

footing and how fast he wishes to go. It would vary also according to the load carried.

The flapping rate of birds is coordinated with the shedding of vortexes from the trailing edge of the wing; these are shed alternately up and down. Many differences in flapping rates occur among species, but the human eye has difficulty counting more than seven or eight flaps per second, so that those for small birds or fast flyers are difficult to obtain. Some average wing-flapping rates per second are given in Table 15·4.

That variations occur with the kind of flying is shown in the averages given in Table 15·5.

Table 15·5

Variation of Wing-Flapping Rate with Flight

Species and Type of Flight	Rate per Second
Blue Jay	
Takeoff	4.0
Steady flight	2.6
Flap-glide	2.2
Bank Swallow	
Coursing	2.8
Climbing	3.7
Cliff Swallow	
Coursing	3.9
Quick-flapping	4.6

Source: Charles H. Blake, "Wing Flapping Rates of Birds," *Auk*, 64(1947):619–620; and Charles H. Blake, "The Flight of Swallows," *Auk*, 65(1948):54–62.

KINDS OF FLIGHT

For convenience and largely in reality also, bird flight may be divided into (1) *power flying*, (2) *gliding*, (3) *soaring*, and (4) *special flying*. The ordinary flight of birds can be considered as power flying, though great variation occurs. Some flight patterns merge or overlap others.

Power Flying. The wings move up and down but with enough additional direction of movement during power flying to propel the bird. The downward sweep on a power flap usually has a forward thrust, with the primaries twisted at an angle to the motion. The resistance of the air against the feathers pulls the bird downward and forward, the power of the wing against the air coming from the great outer breast muscles. But the secondaries also act against the resisting

Table 15·6

Comparison of Depressor and Elevator Muscles of Breast

		Depressor Muscles		Elevator Muscles	
	Body Weight	Muscle Weight	Per Cent of Body Weight	Muscle Weight	Per Cent of Body Weight
American Robin	72.5	10.01	13.90	1.15	1.60
Ruby-throated Hummingbird	2.49	0.51	20.5	0.23	9.25

Source: D. B. O. Savile, "The Flight Mechanism of Swifts and Hummingbirds," *Auk*, 67 (1950):499-504.

air to balance the downward pull of the primaries with the result that the bird moves horizontally, usually with no loss of altitude. The upward stroke receives its power from the inner breast muscles, which are smaller than the outer ones. The weights of breast muscles of the American Robin and Ruby-throated Hummingbird illustrate this (Table 15·6). The latter hovers before a flower and must call upon the elevator muscles to help maintain the bird in the air, which it must do without much aid from the air stream, meanwhile counterbalancing the action of the depressor muscles (Savile, 1950). The Swift has a rather similar wing (Fig. 15·5).

The rotation of the outer primaries and adjustment of the secondaries together during flight give a horizontal thrust for forward movement. Yet despite the fact that the secondaries move up and down with the wing, they give support at all times, whether going up or down. Relative air pressure on the upper and lower surfaces determines the support irrespective of wing direction, though the dif-

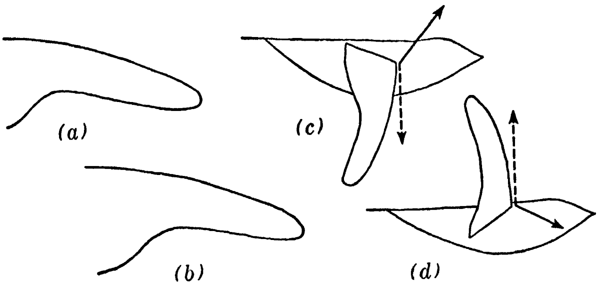

Fig. 15·5. *Wing-shape of (a) Ruby-throated Hummingbird and (b) Chimney Swift; (c) probable wing action of Swifts and Hummingbirds in level flight during down stroke; (d) same during up stroke. (After D. B. O. Savile, "The Flight Mechanism of Swifts and Hummingbirds,* Auk, *67(1950):499-504.)*

ference can be greater on the down stroke. Hence, the wing supports the body more efficiently on the down stroke.

Gliding and Soaring. Gliding and soaring flight differ little except that we consider gliding to be from *a higher to a lower altitude* ("sliding down hill") and soaring as flight by riding rising air currents. Any flying bird seems able to glide if the angle of coasting is steep enough. Thus the American Robin or Mockingbird can glide from a perch down to the ground on set wings. Even the Grouse, which have no soaring ability, can glide from a ridge to the valley floor. (The hunter often calls it "scaling.")

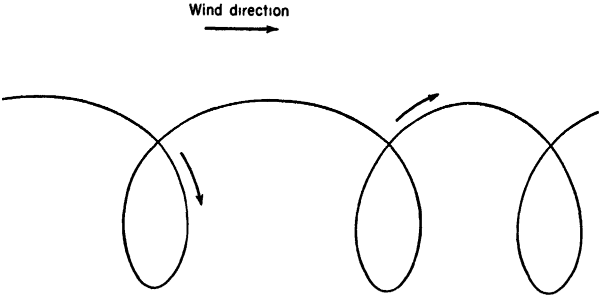

Fig. 15·6. *The path of a soaring Hawk. The arrows show direction of wind and bird, respectively. Note that the bird moves forward more slowly into the wind than with it.*

On sunny days, air rises over warmer surfaces, and sinks over cooler ones. These currents of air (called *thermals*) provide means by which Vultures soar on clear days, in a sense by "sliding down hill" on rising air. They can rise or sink according to the power of the rising air and the advantage taken of it (Fig. 15·6). Warm air rises and cold air sinks, which cause vertical air currents. Rising air currents occur also when moving air strikes any obstruction that deflects it upward. Birds soar along topographic features (ridges, cliffs, shores) that deflect upward the passing horizontal air streams.

How capable the bird may be in soaring depends upon its ability to coordinate its movements as well as its airworthiness. The minimum angle at which a bird can glide depends upon its *sinking speed*, which in turn depends upon the wing loading (Küchemann and von Holst, 1941). The minimum sinking speed of the Turkey Vulture is calculated to be 2 feet per second (1.36 miles per hour) and that for the Black Vulture 2.6 feet per second (1.77 miles per hour) (Raspet, 1950). The maximum lift coefficients of the two birds have been determined to be 1.60 and 1.57, respectively. Just how much power a bird requires to maintain itself in the air, that is, to equal its minimum sinking speed, should be of considerable interest. For the Turkey Vulture, the sinking speed indicates that 0.017 horsepower is needed to keep one weighing 5.5 pounds in the air. The Black Vulture with its higher sinking speed will require somewhat more, which calculates to be 0.019 horsepower for 5.0 pounds. Because power-producing muscle can generate for some time an output of about 1 horsepower per hundred pounds, the Vultures seem adequately powered for their type of flight. In power per pound of weight, they are far more efficient than any power plane devised by man and matched at best only by a high-performance sailplane.

Sea birds also soar in updrafts of thermals, but thermals usually are less abundant over water than over land. Many birds follow the air currents rising over waves, which can be noted by watching birds soar along crests just above the water. Cold air over warm water, as in winter, results in convection currents (though heating of air by the water is low). Hence, these convection currents over oceans are strongest in winter and seasonal variations may account for seasonal shifts of pelagic birds (Woodcock, 1942). Other sources of rising air over oceans occur around islands and rocks; the fact that Gulls ride the air currents around a steamer has long been known.

A marked difference occurs in the soaring mechanics of land and sea birds that probably has special significance. Land-soaring birds spread the outer primaries to form distinct slots, which are absent in soaring sea birds. Presumably the less stable air currents over land make the slotted wings necessary or advantageous. But in gliding, the Vulture closes its wing slots, which thereby lowers the drag coefficient from a minimum of 0.19 to 0.0058 (Raspet, 1950). Soaring efficiency for this species presumably then approaches more nearly that of some soaring birds of the sea.

Special Flight. Various flight patterns of birds may properly be considered as *special flight*, though they may be but variations of ordinary flying. Among these should be mentioned the helicopter-like action of a few birds. Chimney Swifts may flutter up a chimney in the morning or down at night. A Hummingbird may move vertically (Fig. 15·5). Several other birds, such as Larks and Grouse, have been observed to rise vertically in song or drumming flight for short distances (pages 283, 324, 329). Some birds can *hover* in the air to seize an insect, to observe, or for other purposes. In addition to Hummingbirds, hovering has been noted in the American Sparrow Falcon, American Marsh Harrier, American Rough-legged Hawk, Black-capped Chickadee, Golden-crowned Kinglet, Eastern Bluebird, Belted Kingfisher, Horned Lark, Lark Bunting, and many others.

Reverse or *backward flight* seems possible in a few birds. Several birds in fights with their fellows have been noted to move backward in air. But the Hummingbirds use reverse flight as part of their regular daily habit. Hummingbirds withdraw their long bills from flowers by flying backward. Some Flycatchers (Tyrannidae), and possibly a few birds that can hover in the air, have been reported to reverse flight.

SPECIAL ASPECTS OF FLIGHT

Feeding Flight. While birds as a group use their wings to transport themselves from one feeding spot to another, perhaps from limb to limb (as in the Warblers), perhaps 50 miles out to search for food (as in the ill-fated Passenger Pigeon), or perhaps far over the seas (as in oceanic birds), many use their wings to place them directly in touch with their food, in many cases by sheer strength of flying. Swallows feed upon the wing, though they spend much of the day perched as do other birds. Chimney Swifts stay aloft for long periods (page 191). The Nighthawk goes out to feed when the light is low, as at sundown and on dark days. Insect-eating birds that feed in flight tend to have wide bills that admit large insects and make a "near miss" of the target still effective.

Gulls, Terns, and a host of other birds fly over the water until they locate suitable food, whereupon they seize it from the air or alight on the water to take it. In a sense, Vultures act somewhat similarly over land—search from the air until they sight food, then land to feed. Some flights of sea birds in search of food exhibit the highest quality of airmanship. The Leach Petrel makes long excursions far out to sea where it skims along the surface barely above the waves. To take full advantage of the air currents immediately above the sea and especially to hover helicopter-like, it has developed relatively large wing areas. Though of about the same weight as a House Sparrow, its wings are about the size of those of an American Robin or even slightly larger (Table 15·3). Its wing loading is about 0.2 of a pound per square foot, comparable to that of many bats, which range from 0.1 to 0.3 (Poole, 1936). Even a Turkey Vulture has a loading of about 1 pound per square foot. But the superior airfoil of the bird makes possible a greater efficiency with a heavier wing load than that developed by bats. Birds fly faster than bats and a greater wing loading can be used when speeds are higher.

Buzzard-Hawks fly, often by soaring, over the land much as do many waterbirds over the sea, searching for prey upon which to pounce. But the Accipitrines usually get their prey by a sudden charge, giving up if the prey reaches a thicket, though they may pursue through open brush. The Falcons, however, catch their prey by "stooping" after "towering" or by overtaking the prey in open and continued pursuit.

Display, Song, and Courtship Flight. As would be expected, ability to fly has led many birds to evolve flying maneuvers, often most spectacular aerial acrobatics, for display and song purposes (see Chapter 17). Display flights are more characteristic of prairie and tundra birds than of others, but they may occur among birds of treetops, marsh, and shore. Even birds of the brush and woodland may have display or song flights (see Fig. 17·8), as may Ducks and others of the water. Such flights often combine flight action and feather structures, but colored markings avoid parts subject to mechanical strain (Auber and Mason, 1955). Often it is difficult to distinguish display and courtship flight as such; probably all ranges of overlap wipe out any but the most apparent distinctions. Because both are given elsewhere, they will not be discussed fully here. Some species having song, display, or courtship flight are listed below, together with their usual habitat.

BRUSH
Vermilion Flycatcher
Magpie
Mockingbird
Chat
Lazuli Bunting
Song Sparrow

SHORE
Oyster-catcher
Spotted Sandpiper
Knot
Godwit
Phalarope
Skimmer

TUNDRA
Rough-legged Hawk
Ptarmigan
Snowy Owl
Pipit
Lapland Longspur
Snow Bunting

PRAIRIE
Prairie Falcon
Curlew
Short-eared Owl
Horned Lark
Skylark
Lark Bunting

WOODS AND FOREST
Woodcock
Pileated Woodpecker
Raven
Red-breasted Nuthatch
Ovenbird
Crossbill

WATER
Tree Duck
Mottled Duck
Blue-winged Teal
Baldpate
Canvas-back
Dipper

MARSH AND MEADOW
American Marsh Harrier
Snipe
Long-billed Marsh Wren
Bobolink
Red-winged Blackbird
Swamp Sparrow

MIXED HABITAT
American Sparrow Falcon
Mourning Dove
Nighthawk
Hummingbird
Scissor-tailed Flycatcher
Starling

Environment and Flight Modifications. Many flight modifications help make it possible for birds to radiate successfully into the many habitats available. Birds of the open develop highly efficient flight, but those of specialized habitats may sacrifice aerial efficiency for more immediate advantages. The flight of gallinaceous birds is an inefficient type from the aeronautical standpoint, but it serves admirably to get a heavy bird up and with celerity behind an obstructing bush, limb, or tree. While the bird usually does not have to fly far, it needs to make sudden departures on short notice.

Birds requiring fast flight or great aerial agility have developed high-speed wings with narrow, swept-back leading edges, slight camber, and fairing of trailing edges (Savile, 1950). Ducks, Falcons, Plovers, Sandpipers, Swifts, Hummingbirds, and Swallows have independently evolved this type of wing (Fig. 15·5), an example of convergent evolution.

As mentioned earlier, the longer tail of birds that hop from limb to limb, such as the Mockingbird, Chickadee, Chachalaca, and Cuckoo, help to support the body during short flights. They may also help to protect the feet from sudden jars by increased braking power for alighting (Fig. 15·7). The long tail of the Road-runner, however, may not be adaptive but a family character retained from the ancestral Cuckoo; it may help in twisting and turning, nevertheless, as when the bird pursues a lizard or engages in combat with a rattlesnake. Grouse of somewhat similar habitat likewise have long tails, which suggests that the long tail of ground birds may have some functional design.

Large birds like the Canada Goose and White Pelican sometimes spend the night on rivers or lakes from which they must climb over a mountain or canyon wall to feeding grounds. The flocks often circle to gain altitude and sometimes move along the front of a canyon side until they can turn up a gulch or side canyon. Aerial evolutions of such flocks are common sights in many parts of the western states.

Birds that migrate long distances tend to have more pronounced emargination of the outer primaries, which seems correlated with their greater need for flight power. Birds of the open have straight, direct flight, but those of brush or forest may have a more rambling flight. Nomadic birds and those that feed in large flocks often develop a "nervous" type of feeding and flight habits. Flocks of Snow Buntings, Bohemian Waxwings, Grackles, and Bush-tits may suddenly take wing without apparent cause, though the habit suggests a functional character (Miller, 1922).

Owls show several modifications of flight related to their habitat. They fly after dark, though Short-eared and Snowy Owls, for ex-

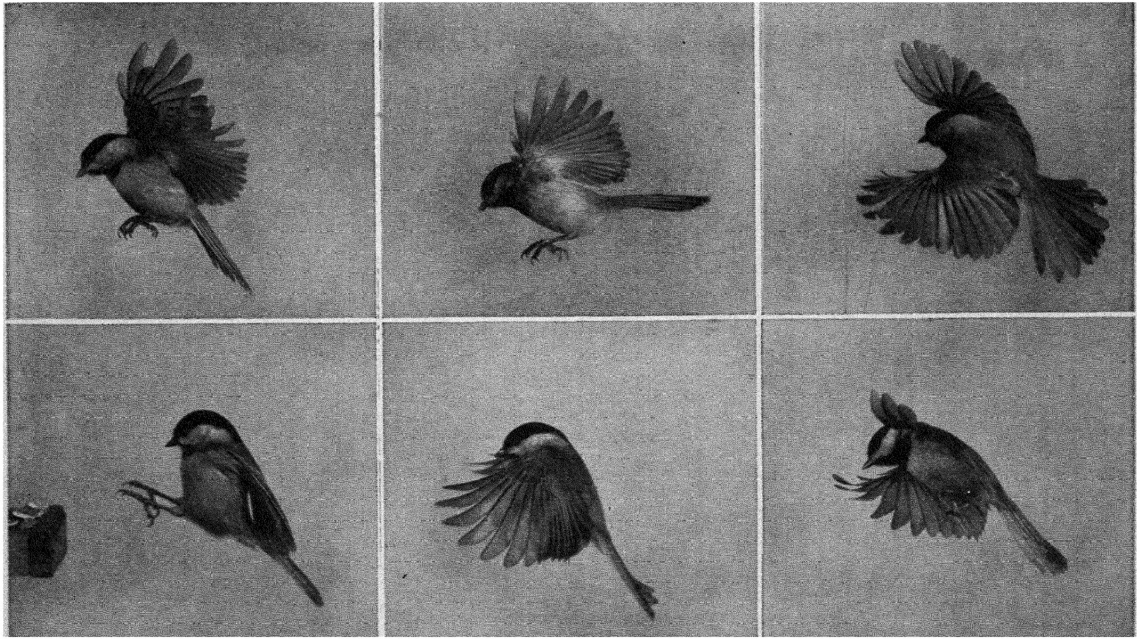

Fig. 15·7. *High-speed photographs of a Black-capped Chickadee coming to a feeding station show the use of wings, tail, and feet. These pictures are not taken in a sequence of the same bird in flight. (Photographed by Crawford H. Greenwalt.)*

ample, may feed in the daytime, especially in high latitudes where the Snowy Owl may see no darkness for weeks. The soft plumage of the feathers serves to deaden sounds made by the passage of the body through the air stream; primary feathers are especially fringed to prevent or to muffle sounds. Because the Owl must usually hunt at close range on account of darkness, it has developed a characteristic, somewhat butterfly-like flight gait.

Flight Gaits. Just as we can sometimes identify a man by the way he walks, so also can we identify many birds by the way they fly. The undulating flight of Woodpeckers, often accompanied by wing noises, is characteristic; Nuthatches have similar flight. The foraging Brown Creeper seldom moves farther than from the top of one tree trunk to the base of another. The Eastern Goldfinch, American Robin, Red-winged Blackbird, and many others fly by a series of quick wing flaps, followed by a short glide. The Eastern Goldfinch alternately rises and falls as it makes a few rapid wing beats followed by a pause. The Red-winged Blackbird rises and falls much less, while Grackles scull across the sky.

A comparison of the flight gaits among several common Swallows of eastern America shows in an interesting way their distinctive manners of flight (Fig. 15·8). The Tree Swallows sail in rather small circles, 20 to 100 feet or more in diameter. Their lower speeds result

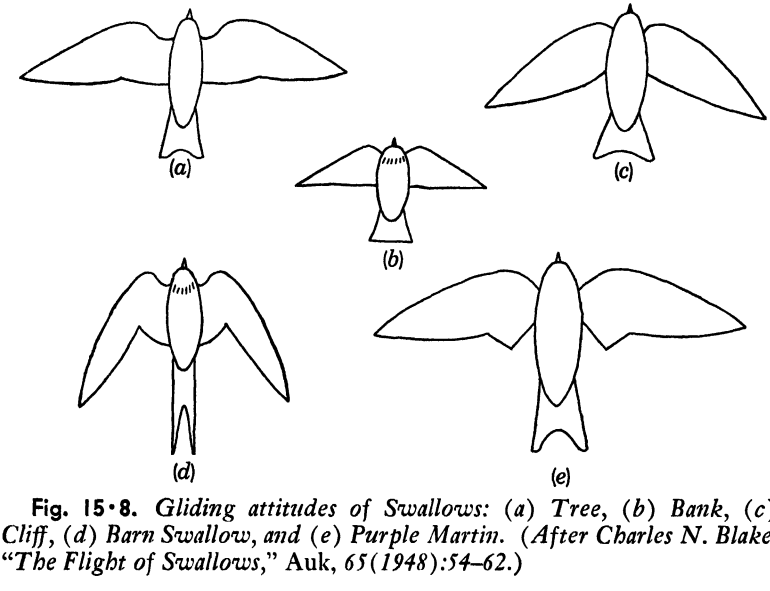

Fig. 15·8. *Gliding attitudes of Swallows: (a) Tree, (b) Bank, (c) Cliff, (d) Barn Swallow, and (e) Purple Martin. (After Charles N. Blake, "The Flight of Swallows,"* Auk, *65(1948):54–62.)*

in apparent unsteadiness and numerous trimming wing flappings. The outstanding characteristic of the Bank Swallow is its fluttery, almost butterfly-like flight; it glides but little or for very short intervals during its irregular flight. The flight of the Rough-winged Swallow resembles that of the Barn and Cliff Swallows more than that of the Bank. The Barn Swallow courses in long runs, often near the ground; it may double back upon its flight path. It glides little if at all, and seems to have two styles of flight: coursing and quick flapping. The flight gait of the Cliff Swallow (page 278) is perhaps best described as intermediate between that of the Tree and Barn Swallows. It uses short glides with downward slanted wings. At intervals in its flight, it climbs steeply on rapidly beating wings, only to dive or flutter downward. The flight of the Purple Martin resembles that of the Tree Swallow; it sails in circles with an alternation of quick flapping and gliding and uses the tail more frequently than other Swallows. Similar variations in flight gaits, including the variable ways the head, wing, tail, and feet are held, characterize birds of close relationship and sometimes those of similar environment. Some bird observers are especially adept at using flight gaits for identifying Ducks, even at the very limits of vision.

Erickson (1955) describes a flight behavior of the Procellariiformes called "Water Walking." In the most common form, the wings act as gliders while the bird runs over the water. The feet may also "run" sometimes in flight, presumably as a vestigial behavior.

Flight Speed. The flight speed has long been commented upon, and some indications of speeds have been accumulated (e.g., Cooke, 1937; Cottam, Williams, and Sooter, 1942; and Meinertzhagen, 1955). The *air speed* of a bird is the speed with which it flies in relation to the air, *ground speed* with relation to the earth. The wind and many other things influence the observed ground speed, so that speed stated for some birds may be incorrect in revealing the actual facts (Allen, 1939). The bird flying in air moves as a part of the air stream. Hence, a bird flying 30 miles an hour *with* a 40-mile wind has an air speed of 30 and a forward ground speed of 70 miles per hour. If it is flying against the wind, however, its air speed would still remain the same but the ground speed would be 10 miles an hour *backward.* If the bird were flying without a "ground" reference (as in darkness), the flying effort would be the same in both cases.

Some average flying speeds for several groups have been reported substantially as follows (ground speed):

Small Passerines	20–37	Starlings	38–49
Corvidae	25–50	Geese	42–55
Shorebirds	35–50	Falcons	45–65

A bird flying at cruising speed may not approach at all near its maximum speed.† In general, the pressed speed is about twice the cruising speed. The slowest powered flight accurately measured seems to be that of 5 miles an hour for the Woodcock. A few examples, presumably correct, of easy or cruising speeds and those under urgency appear in Table 15·7. The maximum reliable speed for any bird is 94.3 miles per hour for a Homing Pigeon (Meinertzhagen, 1955).

Table 15·7

Some Reported Ground Speeds.

Species	Cruising	Pressed
Great Blue Heron	18	36
Black-crowned Night Heron	18	35
Whistling Swan	30	50–55
Canada Goose	44	60
Mallard Duck	40	60
Cinnamon Teal	32	59
Red-head Duck	31	50–55
Peregrine Falcon	37	75
European Partridge	25	41
Bob-white	28	49
Red-shafted Flicker	25	44
Black-billed Magpie	19	35
House Sparrow	24	33

SUGGESTED READING

*AYMAR, GORDON C., *Bird Flight.* New York: Dodd, Mead & Co., Inc., 1935.

HANKIN, E. H., *Animal Flight.* London; Iliffe & Sons, 1913.

JONES, BRADLEY, *Elements of Practical Aerodynamics.* New York: John Wiley & Sons, Inc., 1950.

SHERWOOD, A. WILEY, *Aerodynamics.* New York: McGraw-Hill Book Co., Inc., 1946.

SLIJPER, E. J., *De Fliegkunst in het Dierenrijk.* Leiden, The Netherlands: E. J. Brill, 1950.

*STORER, JOHN H., *The Flight of Birds.* Bloomfield Hills, Mich.: Cranbrook Institute of Science, 1948.

† Reports of high speeds of flight are open to question. The Peregrine Falcon has been reported at 175–180 miles an hour (Cooke, 1937) and a Swift of India at 200 miles an hour (*British Birds*, 16:31, 1922). The observer reporting the latter based his calculation on the time it took birds to fly from his position to a ridge two miles away, behind which he assumed that they disappeared. Tests have shown that even with binoculars birds the size of these Swifts cannot be traced at half the distance reported (page 465).

16

Bird Migration

Although writings, modern and ancient, may speak of the "mysteries of migration," anything really mysterious about migration depends largely on our ignorance. The "mysteries" become fewer year by year. When more facts lie revealed before us, we shall doubtless be able to interpret the workings of bird migration in accordance with known principles and processes, such as of psychology, physiology, geography, meteorology, and physics. Bird migration occurs on so large a scale in high and middle latitudes as to become apparent to all who have contact with nature. The movement over great distances has long challenged the imagination of men, for surely bird migration is one of the most remarkable happenings of all animal life. It is not surprising, therefore, that many explanations (both ancient and sometimes even more recent) of this, as of other biological phenomena, have at various times and places been clouded by superstition, misconception, and fantasy. Though bird migration has claimed most attention, birds are not alone in migrating. The phenomenon of migration will be found throughout the animal world.

CONCEPTS OF MIGRATION

Early Accounts of Migration. Historical accounts tell of early people who remarked upon bird migration and sometimes used it as an indication of the coming of spring or fall. Writings of modern travelers have reported that among primitive peoples of today bird migration marks the advent of a new season, and probably the same may be assumed for prehistoric man. The legends and literature of ancients contain references to bird migration. Thus we find Homer, the *Old Testament*, the *Kalevala*, and the *Sacred Books of the East* commenting upon the passage of birds. No doubt unwritten folklore also mentioned it. Aristotle (B.C. 384–322) wrote of migration and surely must have assembled much of his knowledge from both earlier and contemporary scholars and nonscholars alike. Pliny (23–79 A.D.) included migration comments in his *Historia Naturalis*, much from Aristotle but some his own. It is said that he had available a biological library of 2,000 volumes, so that we may assume he built upon the writings of others along with information then currently available. Little increase in knowledge seems to have occurred during the period of the Dark Ages. Frederick II (1194–1250), however, mentions migration in his famed *De Arte Venandi cum Avibus*, some of his comments being particularly keen.

The industrial revolution brought an increase in avocational natural history as time for leisurely scientific pursuits became available with improved economic and political conditions; our knowledge of bird life, including migration, increased in consequence. By 1703, "a gentleman of piety and learning" had the courage to propound the remarkable fantasy that birds migrated to the moon by aiming in the right direction and flying a couple of months until the moon returned to the target position. Probably the gentleman would have been treated in a most ungentlemanly manner in the authoritarian days of a few generations earlier. Yet a hundred years later, knowledge of the pattern of migration was essentially modern, though many refinements, extensions, and improvements have been added since.

Early Ideas of Migration. Just how some of the early ideas arose to explain the disappearance of birds in the autumn and their reappearance in the spring seems difficult to imagine. Most dealt with the *mechanics* of migration, though some may have been concerned with its origin. No doubt many ideas have not survived to the present time because they were not written or because they were of local distribution. The idea that birds flew to the moon in the fall and back again in the spring, though credited to the "gentleman of piety and learning," probably existed in the unwritten lore of the time.

Origin of the idea of *hibernation* among birds as an explanation for their disappearance in winter seems particularly difficult for us to imagine. It has been suggested that the idea arose from the known fact of hibernation in many animal groups combined with the congregating of Swallows in reed marshes in the fall. Their early morning departure being unnoticed, it might be easy to imagine their settling into the water and mud to hibernate like turtles and frogs. Stories of torpid Swallows being dragged from the mud or caught in fishermen's nets can be credited to tellers of tall tales.

The absence of many summer birds in winter and winter birds in summer gave rise to the seemingly reasonable assumption that one transformed into the other, the idea of *transmutation*. The rise of transmutation seems not at all surprising when we recall that things like supernatural power, fairies, miracles, and magic were part of the beliefs of folk people in many lands, widespread in the past and to some extent still. Because a fairy, according to myth, could change itself into a human being, it seems easy to imagine so simple a magical thing as the transformation of one bird into another. The known molt of some birds into different looking plumages may have helped propagate this belief in transmutation. Many an early writer discoursed learnedly upon the matter.

The apparent weak flight powers of some birds, especially small ones, influenced also the thinking of the time. That larger birds might travel far and over bodies of water, such as the Mediterranean Sea, was held to be possible; the passage of Cranes, Storks, and Geese to the Nile was known. The belief that small birds "hitch-hiked" on large ones accounted for the long journeys by birds of seemingly weak flight. As with hibernation and other natural events, "eye witnesses" were present and able to validate the freighting of small birds by large ones. Eye-witness accounts of impossible happenings and imaginative interpretations of possible ones are not a monopoly of the ancients, as fiction and newspaper accounts of arrivals at missions and of other events of natural history sometimes testify today. Seemingly no less fanciful than the accounts of the ancients are "fossil flight plans" postulating that migration of birds originated in continental drift.

Origin of Bird Migration. The origin of migration belongs to the unknown of the past, and what we may learn of it is limited to deduction from our knowledge of the life of the bird and of other animals. No postulate of the origin of migration can do more as yet than offer us a suggestion. In general, two theories have won some acceptance, largely perhaps because they were novel enough to seem somewhat satisfactory. One theory holds that birds in their northern homes were forced southward by advancing glacial or other unfavorable conditions. With retreat of the ice, birds whose ancestral homes were in the North came back but had to leave each fall. In a sense then, each species annually follows the ancestral north and south movement. The converse theory holds a southern ancestral home and that species pushed northward only to be driven back again, a condition now a racial habit.

Some very definite and real facts make both theories unsound ones. Birds of North American origin, the Warblers (Parulidae) and Vireos (Vireonidae), for example, migrate into South America, which is wholly counter to the theory of return-to-the-southern-ancestral-home (at least from the family view). The several common Grosbeaks and Buntings of the subfamily Richmondeninae, the Hummingbirds, the Tyrant Flycatchers, and the Tanangers appear to have arisen in South America, and their wintering in South America may fit the southern-ancestral-home theory but runs counter to the northern-ancestral-home one. The fact that some members of each group do not migrate, or migrate little, runs counter to both. It hardly seems within the bounds of proper logic to sort out those facts in agreement with each as proof for the validity of the respective theory. The fundamental error of both seems to be considering bird migration as peculiar only to birds of the less temperate parts of the Northern Hemisphere.

The Oropendolas of tropical Panama, for example, leave after the breeding season and return again next year. The White-winged Doves south of the Tropic of Cancer in Mexico move out after the nesting season, just as do those farther north. The Yellow-green Vireo of tropical Central America migrates like its northern relatives. The Gray Kingbird of the West Indies even reaches the Amazon Valley in migration. These few examples serve to show that migration does occur in tropical regions; it may prove far more regular there than has been commonly assumed (Fig. 16·1).

In addition to many land birds, pelagic birds of tropical and subtropical waters also show definite migrations. The Tropic-Bird, Albatrosses, Shearwaters, and others may wander far over the tropical seas yet return to small islands to nest. The Wide-awake of Ascension Island has a habit, remarkable to us, of returning at nine- to ten-month intervals to breed four times in about 3 years (page 358).

Biological Origin of Migration. The fact that seasonal movements occur throughout the entire animal kingdom, both invertebrate and vertebrate, suggests the very plausible working hypothesis that such movements are an inherent part of animal make-up. All gradations occur between the few inches of movement of a tick seeking winter quarters in the forest floor and the great intercontinental migrations of birds. In many cases, the movement of an invertebrate seems just as great a tax on its locomotor powers as the intercontinental journey is to a bird. A snake that slithers 5 miles down a canyon bottom may have made a journey comparable to 200 miles or more for a Dove. The toad that hops 2 miles to a pond for breeding has performed a rather long journey. On theoretical grounds, it seems entirely logical that when amphibians arose from fish, they carried with them a hereditary tendency for seasonal movement that they passed on to reptiles which in turn passed it on to birds and mammals. Even though some fish and mammals migrate (e.g., salmon, eel, bat,

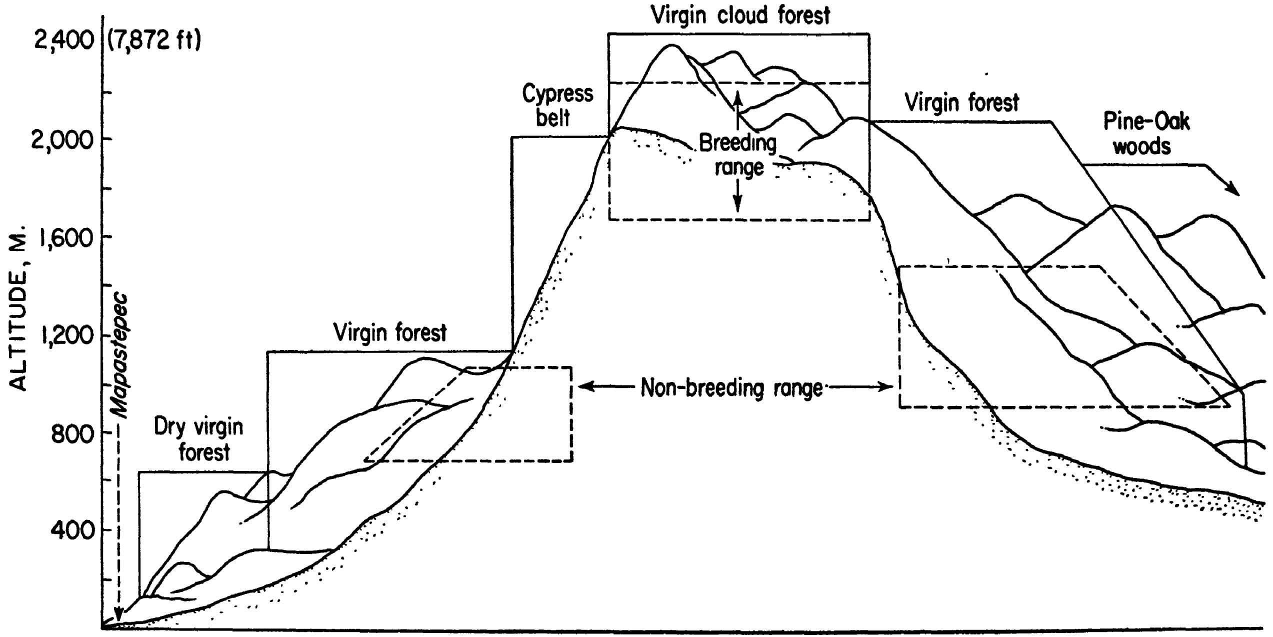

Fig. 16·1. *Diagrammatic cross section through the breeding and non-breeding ranges of the Emerald Toucanet, Sierra Madre de Chiapas, Mexico. Dashed lines indicate the respective range types. The village of Mapastepec, Chiapas, is indicated by the arrow on the left (western) slope. (After Helmuth O. Wagner, "Notes on the Life History of the Emerald Toucanet,"* Wilson Bulletin, *56(1944):65–76.)*

caribou, seal), birds with their great mobility have brought migration to a state of geographic perfection previously unknown. It is possible that bird migration arose by the application of greater distances to an existing biological inheritance of periodic movement during unfavorable seasons.

CONTROLS OF MIGRATION

Internal Influences Controls of bird migration, while more difficult to recognize than those of common activities, seem to center in the nervous and endocrine systems, the two coordinating mechanisms in the body. The over-all control of the endocrine glands rests in the pituitary. Experiments have shown that increase of light through artificially increasing the length of day causes the pituitary to secrete when the glands are increasing in size, as would happen in spring. With the growth of gonadal tissues often goes increased deposition of fat, like fuel being loaded for a journey, sometimes 10 per cent of the body weight in 7 to 10 days (Fig. 16·2) (Wolfson, 1945; Odum, 1949). Probably other functioning parts of the body are likewise brought into migratory adjustment (Seibert, 1949).

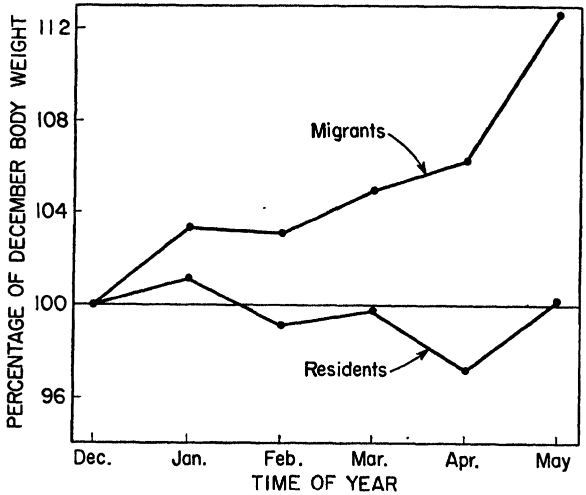

Fig. 16·2. *Migratory birds lay on fat before migrating, often while resident birds are losing it during the stress of the breeding season, as shown by curves of body weight. (After Albert Wolfson, "The Role of the Pituitary, Fat Deposition, and Body Weight in Bird Migration,"* Condor, *47(1945):95–127.)*

When the physiological condition of the bird reaches the right stage for the bird to cope with the strains of migration, release of the appropriate behavior patterns seems to occur (see Fig. 13·1). The migratory tendency and the functioning of the body are inherent behavior patterns set in motion by external, annual stimuli, of which changes in day length are believed to be the most important. Not all birds respond alike; resident birds may not respond as do migratory ones of the same species. Sudden changes seem unable to cause response, which seems adjusted to progressive, slow changes. The stimulation of migration evidently may involve the nervous system as shown in penned birds. Confined migratory birds (and sometimes resident ones also) show signs of tension during the migration season; they are particularly restless during the hours of peak migration (the *Zugunruhe* of Palmgren, 1944).

External Influences. Birds in high latitudes experience a marked change of day length (*photoperiod*) in midsummer when rather abrupt fall migration behavior becomes clearly evident. The shortening of the day, however, is not so noticeable in lower latitudes. The many northern birds wintering south of the Equator raise a definite problem to the assumption that increased day length initiates spring migration. For them, the length of the day decreases instead of increasing as it does north of the Equator. But we are unable as yet to distinguish between possible stimulation by *relative* day length and by *accumulated* day length. The stimulation of the pituitary by day length, either because of increasing or decreasing light, may be a cumulative one regulated by the *total* length of the days. Experiments with captive birds tend to confirm the hypothesis that total day length, within the required limits and following a *refractory period*, stimulates the pituitary (Wolfson, 1952), but the alternation of light and dark seems more effective than continuous light.

Temperature and humidity no doubt influence migration (though the bird is so highly insulated as to be considered rather independent of temperature change). Birds flying northward may be shifted about by wind and storm, so that actual arrival at any spot may be from any compass direction, though the migration itself may be from the south. In like manner, birds may depart in almost any direction from the local standpoint, though the over-all direction is north or south. It may be possible, though we know little about it, that birds migrating in spring can recognize warm, wet air masses flowing northward or cold, dry ones rolling out of the North. The same may occur in the fall. The arrival of unusual numbers of birds and even their appearance off course may correspond with air mass movements as well as with barometric pressures.

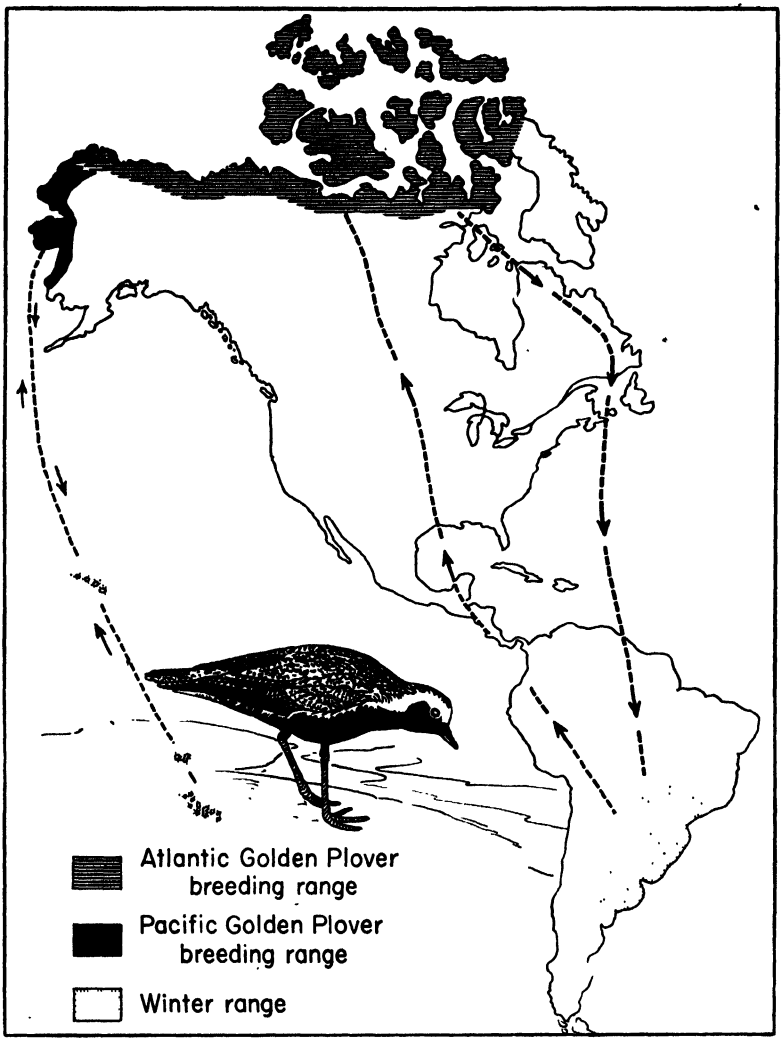
Atlantic Golden Plover breeding range
Pacific Golden Plover breeding range
Winter range

Fig. 16•3. *Adult Golden Plovers migrate, presumably nonstop, across the western Atlantic to South America in the fall and northward through the Mississippi Valley in the Spring. Young birds use the Mississippi route during their first fall. The Pacific Golden Plover and some other species of Alaska and Siberia apparently make a nonstop flight across the ocean to the Hawaiian Islands, Marquesa Islands, and Low Archipelago. (From Frederick C. Lincoln,* Migration of Birds, *U. S. Department of the Interior, Fish and Wildlife Service, Circular No. 16(1950), p. 54.)*

In addition to air masses, the *planetary wind system* also seems to exert a control over migration. The Golden Plover starting from the Arctic, for example, appears to drift eastward in autumn with the prevailing westerlies shifted north with the sun, but they are also being turned southward by deflection, which helps to bring them into the New England and Maritime coasts. It must be recognized also that the birds probably follow landmarks suitable to their instinct pattern. Once taking off south across the western Atlantic, the Golden Plovers should come under the Northeast Trades that bear them into South America, rather than out into the South Atlantic (Fig. 16·3). In addition, they move southwest by deflection. Once across the Equator, the Southeast Trades also tend to drift them westward so that their appearance in Patagonia seems assured. The journey north again drifts them westward, toward Central America rather than the Atlantic Coast. Their appearance on the plains and in the Mississippi Valley thus seems reasonable. No doubt landmarks are used in maintaining a course within the general northward impulse, though local and regional movement may be influenced still by wind, air masses, and storm. But how Alaskan birds (several species besides the Golden Plover) hit Pacific islands is not so readily explained as how those of eastern America hit South America (Fig. 16·3).

MIGRATION HABITS AND BEHAVIOR

Means of Migration. Birds migrate by exactly the same means that they use for ordinary everyday passage—walking, swimming, flying. Many gallinaceous birds, if they migrate at all, migrate on foot. In eastern North America, the Wild Turkey in the early days migrated on foot, perhaps a hundred miles or more, flying only when it crossed rivers or left its night roost. The Blue Grouse of the Western Mountains migrates up the mountain slopes on foot in fall and down in the spring, mostly on foot (Fig. 16·4; see also page 301), a journey that may reach 15 or 20 miles (Wing, 1947). But the Prairie Chicken and Sharp-tailed Grouse fly in migration. Flightless land birds, like the Ostrich and Rhea, perform on foot whatever seasonal movements they may have. Flightless sea birds migrate by swimming. The Great Auk migrated southward along both sides of the Atlantic and at times reached the Middle Atlantic States and France. The Penguins of the Antarctic migrate away from that continent and back again by swimming.

In a few known cases, migrating birds moved by long and rapid daily flights. A Blue-winged Teal (young male) was recovered at

Maracaibo, Venezuela, exactly 1 month after its banding 3,800 miles away in the Athabasca River delta (Lincoln, 1950). A Lesser Yellowlegs banded on Cape Cod, Massachusetts, August 28, 1935, was killed 6 days later on Martinique, West Indies, 1,900 miles away. Its average speed of 316 miles a day establishes a record. Migrating bands of Hawks, moving along the Allegheny ridges may go long distances without stopping. Flights of Herons and Geese have been followed for many miles across country. A banded Turnstone released at 11 A.M. at Helgoland was shot 25 hours later on the North Coast of France, 510 miles away, the fastest flight yet known for a single day. Some flights of homing birds, it might be added, have reached greater daily speeds: 715 miles in fewer than 24 hours for a Herring Gull and 1,000 miles for a racing pigeon (Griffin, 1944, 1952). But most migrations of small birds seem less hurried. The American Robin advances northward hardly as fast as the march of spring. Canada Geese move at about the speed of spring and follow rather faithfully the 35° F. isotherm. The Black and White Warbler averages about

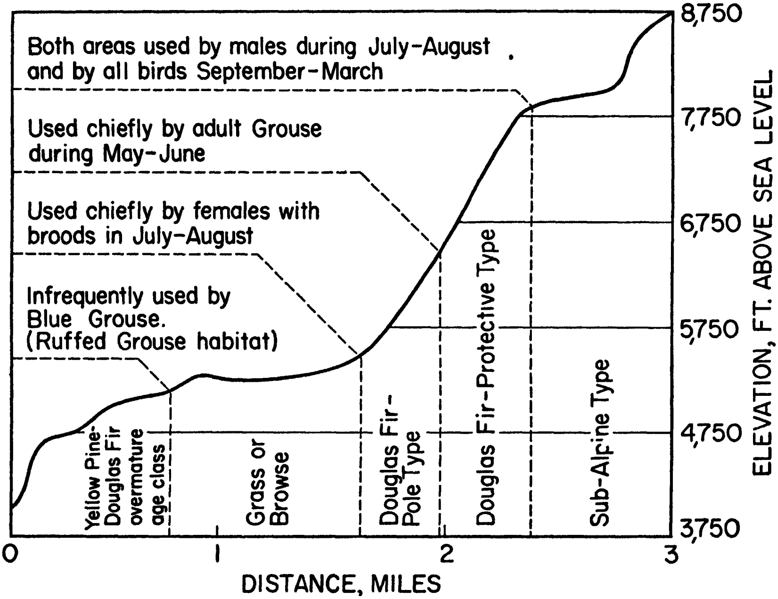

Fig. 16·4. *The summer and winter ranges of the Blue Grouse in Idaho show seasonal preferences. (After William H. Marshall, "Cover Preferences, Seasonal Movements, and Food Habits of Richardson's and Ruffed Grouse in Southern Idaho,"* Wilson Bulletin, *58(1946):42–52.)*

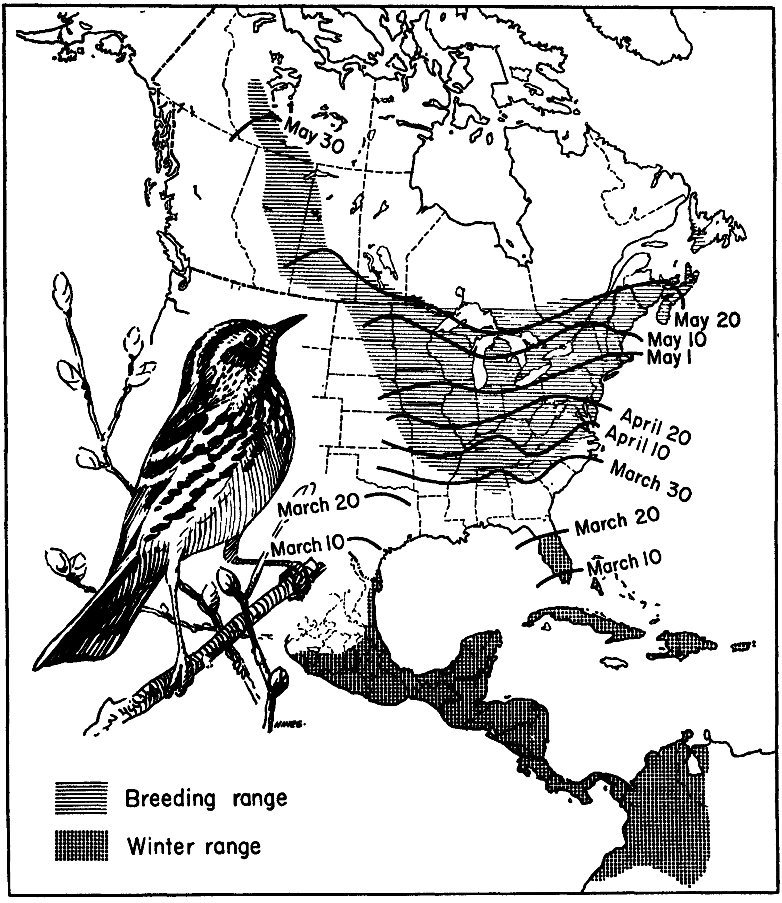

Fig. 16·5. *Breeding and winter ranges of the Black and White Warbler. Isochronal lines show the northward movement. (From Frederick C. Lincoln,* Migration of Birds, *U. S. Department of Agriculture, Fish and Wildlife Service, Circular No. 16(1950), p. 13.)*

20 miles a day in crossing the United States (Fig. 16·5); the Blackpoll Warbler averages 30 miles until near its breeding range, at which time it may speed up to 200 miles a day (Lincoln, 1950). The Gray-cheeked Thrush may average 130 miles a day during its 4,000-mile journey.

A bird may take 6 weeks to cross the United States and then use but 10 days to pass on to Alaska. (Toward the end of migration, birds hurry through in mid-latitudes much more rapidly than earlier in the season. Acceleration of speed as migration draws to a close or as the bird approaches the breeding grounds is a regular characteristic. The mechanism controlling this and the variations involved have been little studied; consequently, we know little of this important acceleration process.

In general, many birds migrate at an average rate of but 30 or so miles a day. Birds may pause in migration, and banders often find their birds repeating for 2 or 3 days or even a week before a new group replaces them. Fall migrations for small birds may be rather deliberate and in easy stages compared to spring. But some birds, such as some Waterfowl, may remain in the North until late and then rush southward. Yet some migrants may move southward very rapidly in early fall.

Kinds of Migration. Migration from areas of severe winters to lands of mild winters has claimed most attention. Yet it appears likely that only some 20 per cent of the world's birds so migrate, with perhaps 60 per cent more wandering at least locally in the nonnesting season. Not more than 20 per cent should be accounted wholly sedentary and fixed the year around. No classification of birds according to migratory habits fits all cases or even the same bird everywhere. A common practice, however, lists birds under such terms as *transients, permanent residents, summer residents, winter residents,* and *erratic wanderers.*

In some birds, as in the Black-capped Chickadee, Song Sparrow, and Cowbird of North America or the Starling, Rook, and Skylark of Europe, some individuals or some populations may be essentially resident while others may migrate. It appears that all gradations occur between long geographic migrations and confinement to a fixed territory the year around. Some birds may in various areas and at various times show several different movements, in some cases staying over one winter and migrating another year.

Local shifts of range occur in many species. To feeding stations in winter come wandering Black-capped Chickadees that banding shows remain in the region throughout the year. Yet careful banding during the winter sometimes reveals two or three complete or nearly complete replacements by influx of new birds and departure of familiar ones. It has been presumed that the more sedentary birds are older ones. In the American West, Prairie Falcons may move out into the open fields in winter, though the rest of the year may be spent near bluffs and other nesting sites. Birds of the forest abandon the more exposed (especially more windswept) areas and pass to the thicker timber in winter. A particularly cold period, as occurs with passage of a cold air mass, may bring about a shift to more protected cover. There may be daily or seasonal shifts to warm layers of air in mountain regions. Cardinals sometimes move in winter to brushy river bottoms and Song Sparrows to cattail marshes. Coveys of Bobwhites gather in fall and wander rather systematically over a circumscribed winter range.

In mountain regions, many birds shift in winter from higher to lower altitudes. The birds of higher reaches move to lower altitudes and foothills and sometimes far out on the adjoining countryside. In the Rocky Mountains and Cascades, Juncos, Grosbeaks, Rosy Finches, and others reach the lower altitudes in large flocks in fall and winter. The Rosy Finches may drop 10,000 feet or more in altitude yet move scarcely a hundred miles. Parallel shifts in the Tropics have been reported; the Emerald Toucanet breeds near the tops of the mountains from November or December to May or June and passes the nonbreeding season in the lower altitudes (Fig. 16·1).

The Clark Nutcracker of western forests breeds early in summer and moves upward with the advance of summer but returns before winter. The Blue Grouse, however, reverses the usual practice and descends to breed in the low altitudes and moves back to winter again in the high altitudes (Fig. 16·4). The birds trek on foot, during the downward journey occasionally flying across open slopes.

Sporadic migration seems to occur in some species. Pallas Sand Grouse often "irrupts" out of the central Asia dry lands in a northwesterly direction to reach Europe and even the British Isles. Among the invasions known were large ones in 1863, 1888, and 1908. Under sporadic migration may perhaps be grouped such events as the invasion of North America by Lapwings from Europe, as well as the European Widgeon (though the latter may breed in small numbers somewhere in the eastern, New World Arctic). The Thick-billed Parrot invaded southern Arizona from Mexico in July, 1927.

Accidental occurrence may be of the same nature as sporadic migration, but most likely it indicates birds blown off their courses, those that may have missed or overshot the mark, and some that are probably confused wanderers.

A special kind of migration in the Shelduck of Great Britain has been termed *molt-migration* (Coombes, 1950). During July, even before many young are flying, almost all the adults depart from the western side of the island to the eastern side by definite routes, showing great reluctance to fly over land. There they pass through the summer molt, during which time they become flightless like other Ducks and Geese. The birds drift back again slowly over a period of six months.

Still another movement that must be considered when dealing with migration goes under the name of *nomadism.* True nomadism involves absence of a fixed home and breeding wherever and whenever conditions are suitable. This condition seems to be met in part by Crossbills, especially the Red Crossbill, in eastern North America and parts of Europe and perhaps of Asia. The Crossbills wander over the forest and nest in areas having a good cone year. They have even nested away from the conifer country, perhaps because of cone failure. Nesting has been reported for every month of the year, though most nesting still occurs during early spring.

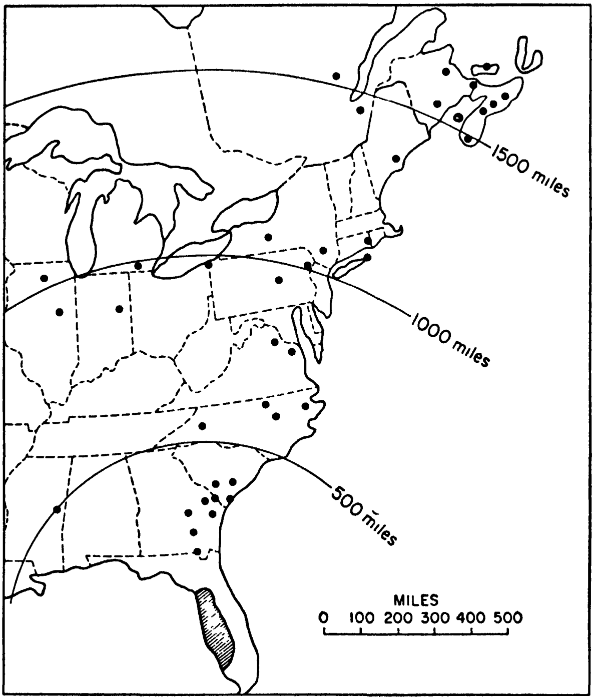

Fig. 16·6. *Recoveries of Bald Eagles banded in Florida, mostly as nestlings, show a northward movement after the nesting season. (After Charles L. Broley, "Migration and Nesting of Florida Bald Eagles,"* Wilson Bulletin *59(1947):7.)*

The postseason wandering of young birds, especially the northward movement of young Herons, Egrets, Gulls, Bald Eagles, Mourning Doves, and others, has been termed *vagrant migration* (Fig. 16·6).

How widespread it may be is not known, but it may very well occur, at least occasionally, in most families of larger birds and perhaps others also. Banding returns indicate that it occurs more often than previously thought to be the case.

Flight Years. To speak correctly, we should probably refer *flight years* to sporadic migration. The Crossbill has already been discussed as nomadic. Whether called nomadism or sporadic migration, flight years are so well known in a number of northern birds as to demand special recognition. No doubt all gradations can be found between migration and the invasion so striking as to be called flight years.

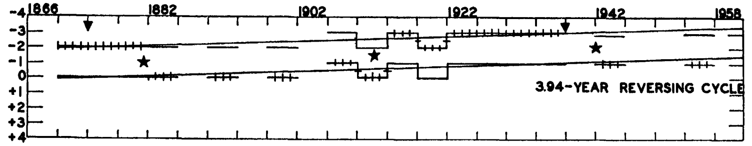

Fig. 16·7. *A 4-year time chart of the Pine Grosbeak flight years in the Great Lakes area shows a reversing cycle of 3.94 years. The rise of one year in the sixteen intervals between the arrows indicates a "false length" of one-sixteenth year shorter than the time chart intervals. The reversal points are marked by stars. Two cycles, one 4.222 years long and another reversing cycle of 3.69 years, are associated with this behavior. A reversing cycle is a wave behavior known also as a "beat." (From Leonard W. Wing, "Global Pattern of 4.222-Year Cycles in Temperature,"* Journal of Cycle Research, *3(1954):55–83.)*

Flight years of the Snowy Owl in eastern North America occur at about four-year intervals in a well-marked manifest cycle (Gross, 1947). Those of the Northern Shrike are similar. Snowy Owl flights occurred in 1833, 1837, 1839, 1846, 1853, 1862, 1866, 1876, 1882, 1886, 1889, 1892, 1896, 1901, 1905, 1909, 1912, 1917, 1921, 1926, 1930, 1934, 1937, 1941, 1945, and 1949. Among other birds having similar flight years are Goshawk, Bohemian Waxwing, Evening Grosbeak, Pine Grosbeak, Red Crossbill, White-winged Crossbill, and Red-breasted Nuthatch in North America. Similar northern birds have flight years in the Old World, often the same or related species in the two continents. Flight years may also involve desert or dry land birds (though perhaps not in America). The Sand Grouse has long been known for this behavior.

The flight years of the Pine Grosbeak in the Lake States (Fig. 16·7) averages about 3.94 years apart as the result of two or more cycles (Wing, 1954) (which in turn is compounded of two or more other cycles). One cycle measures 4.222 years long and another

3.767 years. In some species, the flight years may occur rather markedly every other year and show evidence of two-year cycles or alternations. Alternations were reported in the nesting of the Passenger Pigeons and were related to setting of the acorns the year before (Schorger, 1937). (Some alternations in the plant world may be related to carbohydrate exhaustion, as in fruit trees, though we know little of it in the wild. Some alternation of breeding success of animals has been termed "inversity.")

Altitude of Migration. Birds migrate at low altitude and few migrate at distances more than 3,000 feet above the ground itself—in fact, most migration passes within a few hundred feet of the surface, be it water, trees, or ground. Birds passing over the open sea have been reported flying close to the waves, which can also be noted in birds migrating along coasts. It seems entirely likely that the bulk of migration occurs at levels under 300 feet or so above the surface. Observations of migrating birds, scanty though they are, indicate that birds follow the ground level, rising over ridges and dropping down into valleys. An observer in Abyssinia reported Swallows clearing a 10,000-foot ridge and passing down into the valley below. Since the country beyond the valley also was high, it must be presumed that the birds rose again on the far side of the valley. Birds riding the air currents along the windward side of mountain ridges may be expected to pass at any altitude, though their distance above the slopes is low. In the same way, birds may cross a narrow valley to ridges on the far side without losing altitude. Ridges of the Cascades reaching nearly 8,000 feet have been cleared by Canada Geese without dropping into a valley bottom 2 or 3 miles wide and but 1,200 feet in altitude. Migrating Cranes have been reported over the Himalayas at heights in excess of about 14,000 feet (perhaps as high as 20,000 feet); the height above the surface still probably did not exceed 5,000 or 6,000 feet.

Diurnal and Nocturnal Migration. Most birds in migration show definite tendencies to be either *diurnal* or *nocturnal*, but some may be both. In general, birds of strong and direct flight, those of the open, those of large size, and those that can feed on the wing tend to migrate chiefly in the daytime. Birds of weaker flight, those of the brush and woodlands, those of small size, and those that must search for small food items near the ground migrate chiefly at night. Waterfowl and Shorebirds have long been known for their habit of migrating at night, especially on clear nights, as well as during the day. A list of probable nocturnal and diurnal migrants compiled from various reports is given below:

Nocturnal Migrants

Rails, Coot
Cuckoos
Whip-poor-will
Woodpeckers
Flycatchers (short-tailed)
Wrens
Thrushes
Kinglets
Vireos
Warblers (New World)
Bobolink
Orioles
Tanagers
Grosbeaks (Neotropical)
Sparrows (native)
Buntings

Diurnal Migrants

Loon
Pelicans
Storks
Vultures
Hawks
Grouse
Cranes
Gulls
Doves
Nighthawks
Swifts
Flycatchers (long-tailed)
Kingbirds
Swallows
Longspurs
Chickadees
American Crow
American Robin
Bluebirds
Pipits
Waxwings
Shrikes
Starling
Blackbirds, Cowbirds
Purple Finch
Grosbeaks (Boreal)
Redpoll
Goldfinch, Siskins
Crossbills

Either or Both

Herons
Egrets
Shorebirds
Geese
Ducks

Flocks of migrating Geese, Crows, and Blackbirds are common sights over favored routes in eastern North America. Nighthawks migrate in large circling flocks, feeding as they go, wending their way always toward the ultimate destination. Grackles pass in long streaming flocks. But no doubt mass migration reached its greatest heights anywhere in migrations of the Passenger Pigeon which formed

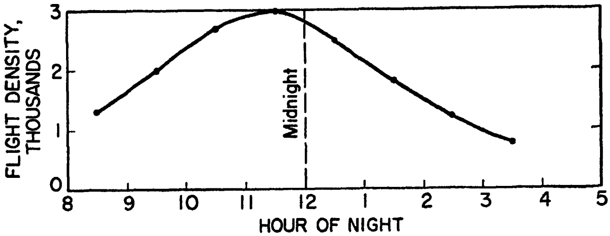

Fig. 16·8. *Average hourly densities of birds observed by telescopes sighted on the full moon, based on Central Standard Time (90th Meridian Time). (After George H. Lowery, Jr.,* A Quantitative Study of the Nocturnal Migration of Birds, *University of Kansas, Museum of Natural History Publications, 3(1951):361–472.)*

great rivers of living birds, miles wide and miles long, hundreds of millions of birds streaming onward (page 256).

Regular night migrants move in scattered fronts across the night sky. Thousands of birds may pass over in the course of a single night to descend to earth by the coming day. The sudden appearance of birds on any one day in the spring reflects arrival during the previous night. The training of telescopes against the moon during the nights of migration reveals this parade across the night sky (Lowery, 1951). The flow varies with the hour, place, season, and power of migration. In general, the rate of nocturnal migration increases from dark until near midnight when it reaches its peak (Fig. 16·8). Studies in Europe show that the greatest diurnal migration activity occurs after dawn and again in late afternoon, somewhat appropriately similar in pattern to night migration (Thomson, 1953), as well as normal diurnal activity.

Advantages of Migration. It may be taken as axiomatic that a phenomenon of such magnitude as migration has corresponding advantages to the participants. The travels of most high-latitude migrants clearly makes it possible for them to occupy range suitable in the summer even though it may be wholly unsuitable in winter. Biological energy resources being what they are, high latitudes have their highest energy potential in summer, whereas equatorial regions have uniform resources, save for marked wet-dry season differences. Hence, the nearer one approaches the Tropics, the more nearly uniform becomes the yearly energy distribution and the less becomes the migratory tendency, though we must not overlook movements during the nonbreeding season in low latitudes. Migration enables birds to utilize the cold latitudes in summer, for example, though they must go elsewhere for winter.

An alternative to migration is *hibernation*, a method used by many reptiles, amphibians, and mammals. Authentic cases of torpid condition during inclement weather, however, have been reported for one or more Goatsuckers (Caprimulgidae).

It seems entirely probable that many birds migrate farther in the fall than absolutely essential for their basic needs. Many Flycatchers pass on to the Tropics, though the Eastern Phoebe stays farther north. Some Shorebirds and others may scatter out along coasts from the United States to Argentina. However it may have arisen, this winter spread may act as a safety device to prevent local overabundance and to distribute the species and family pressure more widely.

Disadvantages of Migration. Migratory birds face many dangers and there is always the possibility of encountering catastrophe as they travel. Storms have brought catastrophe to birds and at times thousands, even millions, have died. A bird resident in familiar surroundings would surely seem to have an advantage over one in strange places.

Many migratory birds fly into towering objects at night, and the loss at some lighthouses has been high. The erection of perches has helped to prevent loss by allowing birds to rest and by reducing hovering flight, laborious for birds; change of the light to red is said to reduce, even eliminate, bird destruction. Many birds have flown into the Washington Monument, towering 555 feet skyward, but the number declined with growth of the city and consequent improved city illumination. At times, birds have crashed against giant skyscrapers in cities.

(Some birds may arrive in the North only to be caught by a late storm and suffer hardship or annihilation. Particularly unfavorable cold in the winter range may also cause great loss. In the same way, migrating birds may run into an unseasonable storm. Many cases are known where such a condition resulted in great mortality and brought about reduced breeding populations for a few birds in some parts of the breeding range later.) Unusually severe winter storms sweeping into the southeastern states have killed many birds, and their loss meant a scarcity in some of the northeastern states for some years.) A "norther" across the southeastern parts of Texas and adjacent Louisiana in February, 1951, for example, brought death to Mourning Doves, Mockingbirds, and many others.

Exhaustion from weariness of flight probably does not occur except possibly when a bird crosses a large body of water, or when it flies under unusual circumstances that drain its energy before replenishment by feeding. The stored energy of the Ruby-throated Hummingbird has been assumed to give it a flight range of 835 miles (Pearson, 1950). The popular notion that birds always return from distant lands exhausted by their efforts seems to be erroneous, yet we should expect some birds to die along the route.

Migratory Navigation. Navigation by migrating birds has been confused with homing by nonmigrants (e.g., Homing Pigeons) and with birds carried away from their homes (such as nesting Gulls, Ducks, and others). While probably related, the navigation of migrating birds, sometimes for the first time, over unknown land to unknown winter grounds, is a different thing from returning to a home from which only recently removed. Nocturnal migrants, like any airborne body, may drift with the flow of air, which in southern parts of America and Europe means an easterly drift with the prevailing westerlies. Like other moving bodies, they are influenced by the forces of deflection (Coriolis force), to the right in the Northern and to the left in the Southern Hemisphere.

Many diurnal migrants clearly show the influence of terrain as they migrate up river valleys, along shores, mountain ridges, and from favored cover. Sometimes this causes a reverse migration locally. Birds migrating northward around the "thumb" of Michigan may swing southward along the western side until they reach Sand Point, over which they go before launching their northward flight across Saginaw Bay. The concentrating effect of points in lakes and bays have long been known. Keweenaw Point (Lake Superior), Sand Point (Lake Huron), Fish Point (Lake Huron), Dorr Peninsula (Lake Michigan), Cape Cod (Massachusetts), and Cape May (New Jersey) have been famed for years as favorable observation places. Points of vegetation in desert regions, groves in prairies, islands in bays, and even mountain peaks concentrate birds in migration.

Nocturnal migrants, too, seem influenced by terrain, for even at night, shadows show the ground pattern. Birds fly less on cloudy nights than on clear ones; they may run into storms or fogs and thereupon become confused and lost, chiefly because they have lost contact with the ground. Sometimes birds flying over cities, especially in fog, become lost, probably for the reason of pattern change. Light below where it should be dark, and darkness above where it should be light, presumably cause loss by the birds of their plane of reference. With sufficient visibility, the bird seems no more confused than in flight at twilight.

Theories of Bird Navigation. Many theories have been advanced to account for birds finding their way. One involves a "mythical sense of direction," but nothing of this sort is known (except in the memory itself). Just as some people seem better able to keep direction than others, birds may be better than most other animals. It has been suggested that young birds learn from the older members of the flock, but for some species serious objections can be raised to this view. Night migrants do not seem to travel in flocks as diurnal migrants do, and unless in compact flocks, they probably could not follow each other except by vocal contact. In any event, the young of some birds migrate separately; the young Cowbird, for example, would hardly be expected to migrate with its foster or biological parents. Most young Golden Plovers, *in fall* migrate to South America through the American interior, while the adults cross the western Atlantic (Lincoln, 1950). Next year these young would be adults migrating over the ocean.

Birds that fly long distances (even across water bodies to land beyond the limits of vision, setting course to objectives a hundred and even thousands of miles away) cannot be credited with ocular navigation. Birds close to the ground have a limited horizon; those swimming in water like the Penguins would see ahead perhaps but a few hundred rods.

Birds may be able to identify air currents by their quality or directional flow when ground reference is present. They have no known way by which to sense or to be influenced by magnetic lines of force. It has been suggested that radar rays may influence them, though these are unknown in nature. That birds detect the earth's deflection (Coriolis force) has been suggested, though no known structure for such detection of deflection exists. Aerophysicists estimate that the bird would have to be sensitive to one part in a million of gravitational acceleration in order to navigate by such force. Air turbulence would mask any signal of such a low order. In any event, the action of Coriolis force is a deflective one acting upon all moving objects, inanimate and animate alike. The movement of air in the tympanic cavity of the ear has been proposed as one possible detection method (Beecher, 1951a).

The direction of bird migration in the Northern Hemisphere is chiefly equatorward in the fall and poleward in the spring. Young turtles are reported to move toward light horizons in making their way to water. Bees have been found to use the angle of light to orient themselves (menotaxis). It is suggested that birds also may use a form of *sun navigation* (Kramer, 1952; Matthews, 1955). (The *pecten*, a structure in the eye, is suggested as the device involved.)

The wintering of northern birds south of the Equator raises a difficult point in explaining bird migration. One attempt suggests a totality of daylight, rather than immediate increase. Perhaps for now we should still consider migration among birds of northern and middle latitudes as a directional response, forward and back with the respective seasons. The actual control mechanism itself is surely a most complex one, not necessarily operating alike for all birds or at all times. The directional controls of the cycle need not be the same throughout the season, even in the same bird. So far as finding their way is concerned, the geographic cues available (such as wind, landmarks, vegetation, topography, skylight, sun) seem sufficient to provide all the guides necessary if the birds can detect such cues.

THE GENERAL PATTERN OF MIGRATION

Migration Pathways. The migration routes of birds form such an integral part of the migration pattern that it seems hardly possible to discuss them separately, so that the subject actually has been cov-

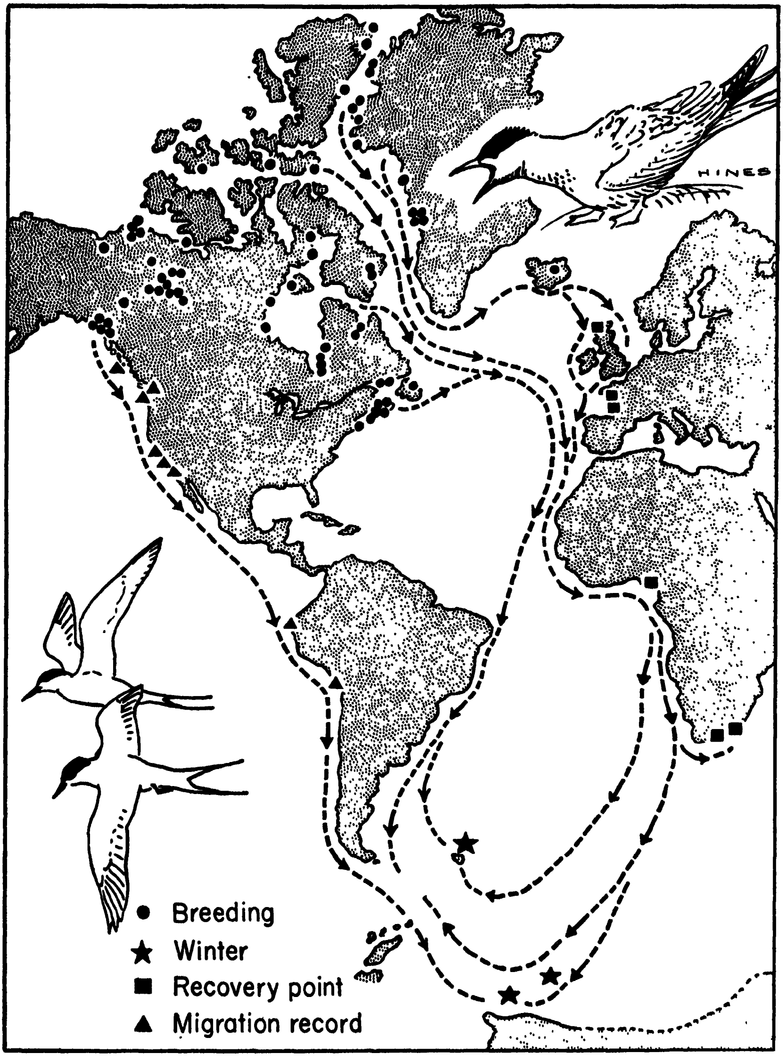

Fig. 16•9. *The route indicated for the Arctic Tern is unique; no other species crosses so freely over the Atlantic between the Old and New Worlds. The extreme summer and winter homes are 11,000 miles apart, so that some Terns probably fly at least 25,000 miles a year. The recovery points represent birds banded as nestlings in North America. (From Frederick C. Lincoln,* Migration of Birds, *U. S. Department of the Interior, Fish and Wildlife Service, Circular No. 16, p. 39.)*

ered already. A few points need to be elaborated upon, and it may be profitable to mention some unusual examples.

The thought of "flyways" developed when banding returns first began to confirm the idea that birds tended to follow regular directions. But the idea of four great Waterfowl "flyways" proves to be a better administrative convenience than a biological actuality. The four "flyways" envisioned as realities were the Pacific, Central, Mississippi, and Atlantic. Their prime use is convenience in dividing up the continent for Waterfowl regulations.

Migration pathways and flyways can be seen on every hand during the passage of migrants at the height of the season. Birds will work through the woods in a flock and follow out along fence rows or concentrate in points of brush before striking out across the open. Coastal margins, points of timber, and land reaching out into marshes and bays are well-used pathways. Coasts themselves form important flyways for birds. Water birds often follow rivers for long distances, even faithfully following river bends though it would be easier to cut across them. But some may cross mountain ranges to shorten distance. The Ross Goose migrates down the eastern front of the Rockies from its restricted breeding grounds in the Perry River district before crossing to its restricted winter range in the interior valley of California.

The round-trip flight of the Arctic Tern from its North American breeding grounds to its winter home in the Antarctic and Sub-Antarctic has long interested people (Fig. 16·9). The birds of northwestern North America migrate down the Pacific coast of North and South America. Those of the eastern half of the Continent cross the North Atlantic and pass down the European and African coasts. Some again cross the South Atlantic below the Equator to the New World side. This species thus spends its summers and winters in regions of continuous or near continuous daylight. It is truly said that it holds the record for all life in the amount of daylight seen. It also holds the record for distance, the extremes of its summer and winter homes being some 11,000 miles apart, which would mean perhaps 25,000 miles of flight a year. The bird also holds the known record for distance of recovery, a chick banded in Labrador, July 23, 1928, having been recovered in Natal, Union of South Africa, November 14, 1928, some 8,000 or 9,000 miles distant.

Premigration Events. Some of the events preceding migration, either spring or fall, have already been touched upon. But from the number of unknowns, it is obvious that a considerable amount of patient field observation in well-known regions as well as distant lands still lies ahead.

The recognizable prelude to migration in many birds, particularly diurnal migrants begins with flocking together in summer, near the end of the nesting period (page 237). In part this may be assembling because of favored habitat. A recognizable nervous tension is evident in the early fall among migrant birds in the North and in early spring among northern birds wintering in the South. Similar happenings occur in tropical winter ranges of northern birds. This state of evident tension can be taken as an indication of impending departure.

Observation of the southward departure of the Cliff Swallow near its northern limit has indicated some of the premigration events. Noticeable shortening of the day takes place by early August, though temperatures remain about the same except for greater coolness at night. Swallows not encumbered by care of young and the young on the wing increase their daily flight both in distance and time in the air, perhaps somewhat as an athlete prepares for a contest. A few ~~warm~~ days may slow up this "preparation," but a few cold ones will increase activity. The day before departure may be one of considerable excitement, birds coming and going all day long with much twittering, often far into the night. On the morning of departure, flocks wheel about the sky in great sweeps, now and then taking off in a general southerly direction, the exact compass bearing within the southerly direction depending upon valleys and ridges. By 2 hours after sunrise, none but nonflying young and their parents remain. A late-rising ornithologist might assume that the birds left during the night; dawn departure of many diurnal migrants may be more common therefore than we suppose.

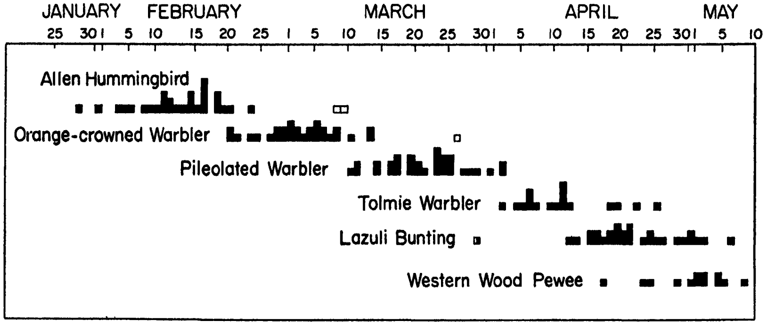

Fig. 16·10. *Spring arrival dates of summer residents in the Berkeley, California, area (1911–1947). Solid block squares indicate first-seen records; half squares, probable early vagrants; open squares, doubtful first-seen records. (After Henry G. Weston, "Spring Arrival of Summer Residents in the Berkeley Area, California,"* Condor, *50(1948):81–82.)*

Spring Migration. Migration (both spring and fall) follows a definite order. Some species migrate early, some late, some in between (Fig. 16·10). A 5-year average at one place will generally show the arrival order of the various readily observed species (Table 16·1).

Table 16·1
Average Dates of Arrival of Swallows, Ann Arbor, Michigan

	Number of Years Reported		Average Arrival		Arrival Sequence	
Species	1880–1905	1906–1930	1880–1905	1906–1930	1880–1905	1906–1930
Tree Swallow	15	25	April 10	April 5	1	1
Purple Martin ...	14	25	April 15	April 8	2	2
Barn Swallow	17	25	April 16	April 15	3	3
Bank Swallow	8	25	April 24	April 21	4	4
Cliff Swallow	14	16	April 29	April 24	5	5
Rough-winged Swallow	2	24	April 30	April 26	6	6

Source: Based upon data from Norman A. Wood and A. D. Tinker, Fifty Years of Bird Migration in the Ann Arbor Region of Michigan, 1880–1930, Occasional Papers of the Museum of Zoology, University of Michigan, No. 280.

On the basis of the few species studied in detail, it appears that in general, males arrive before the females and old birds before first-year ones. The order in 1911 for the Red-winged Blackbird at Ithaca, New York, follows (Allen, 1914):

Vagrants: February 25–March 4
Migrant adult males: March 13–April 21
Resident adult males: March 25–April 10
Migrant females and immature young: March 29–April 24
Resident adult females: April 10–May 1
Resident immature males: May 5–June 1
Resident immature females: May 10–June 11

It seems entirely likely that studies of other species in other localities would be productive of similar results. The northward advance of the hardy birds follows close upon the departing heels of spring. Phoebes, Geese, and Mergansers in America may follow close upon the melting of ice and snow. The Cliff Swallows move northward and northeastward from their path through Central America and Mexico as they come up from South America (Fig. 16·11). The European migration of the Barn Swallow shows a parallel thrust along the west coast of Europe, where it averages about 35 miles a day.

Spring and fall migration through the Mississippi Valley deserves special mention. Topography, vegetation, and wind in concert with position "funnel" migrating birds up and down the Mississippi Valley, which has been called the greatest migrating flyway on earth. Nowhere else will birds be found in such numbers over so wide an area; nowhere else do the birds pass by in such waves of moving life as in this great area extending from the Plains to the Appalachians.

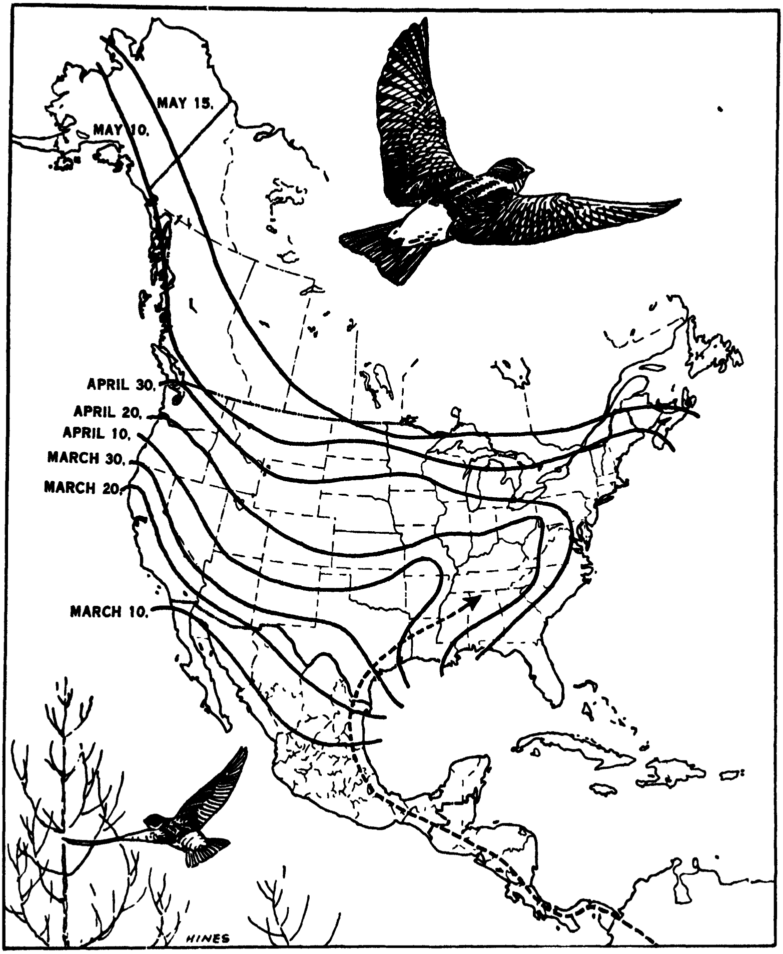

Fig. 16·11. *The Cliff Swallow moves around the Gulf of Mexico. Being a diurnal migrant, it feeds as it flies. Though western records are few and migration in the West somewhat conjectural, isochronal lines have been drawn to indicate earlier arrival in the West and retarded arrival in the East. (From Frederick C. Lincoln,* Migration of Birds, *U. S. Department of the Interior, Fish and Wildlife Service, Circular No. 16, p. 17.)*

Fall Migration. Fall migration may start immediately after the young leave the nest, but some species may wait until later. Many Shorebirds return to the northern states from the Arctic in July, shortly after the last group going north has passed. Adults of some species desert the young and depart south from northern breeding grounds and let the young shift for themselves. Canada Geese, however, tend to migrate as a family unit, while the Cliff Swallows migrate as a colony or part of a colony. Swallows tied down by care of young sometimes remain behind while other individuals of their species that have finished nesting move on. In colonial birds especially, some desertion by parents with weak family ties may take place.

The *sequence of species* in fall resembles somewhat that for spring and the average for a 5-year period is likely to be about the same as for other years. Early fall migrants may depart long before the coming of cold weather; the Blue-winged Teal migrates early, for example, often beginning in August. In the same way, the Bobolink starts southward about mid-August; it moves southeastward into the eastern Gulf states and continues across the Caribbean into northern South America, where the first birds arrive before the middle of September. The winter home in northern Argentina and adjoining regions is reached sometime in November (Fig. 16·12).

Migration and Winter Range. The habitat chosen throughout the year remains substantially similar for most birds. Birds of the brush migrate and winter in brush, while those of the open use open habitat. Some adjustment manifestly must occur, as in birds like the Warblers of the coniferous boreal forest that winter in broadleafed tropical regions.

A bird that has once wintered in an area is likely to return again another winter, just as nesting birds return to their previous residence. Young raised in an area from eggs obtained elsewhere tend to return to the place of rearing, not where the mother laid the egg. The recovery of banded nestlings from the same nest often shows them to have wintered far apart. A brood of European Widgeons banded in Iceland scattered far, some being killed in Europe and some in the United States. While this is a case involving exceptionally long distances, the recovery of many brood-mates indicates clearly that they tend to scatter. But we are ignorant of the system involved, if any.

The fixity of both winter and summer range, when once established, is important and may bear upon problems of the bird's life. No doubt return to familiar territory is an advantage in winter as well as in summer. It seems likely that some entire local populations may migrate and winter together. Geese migrate back and forth as family units and probably community groups also. Their exact path and

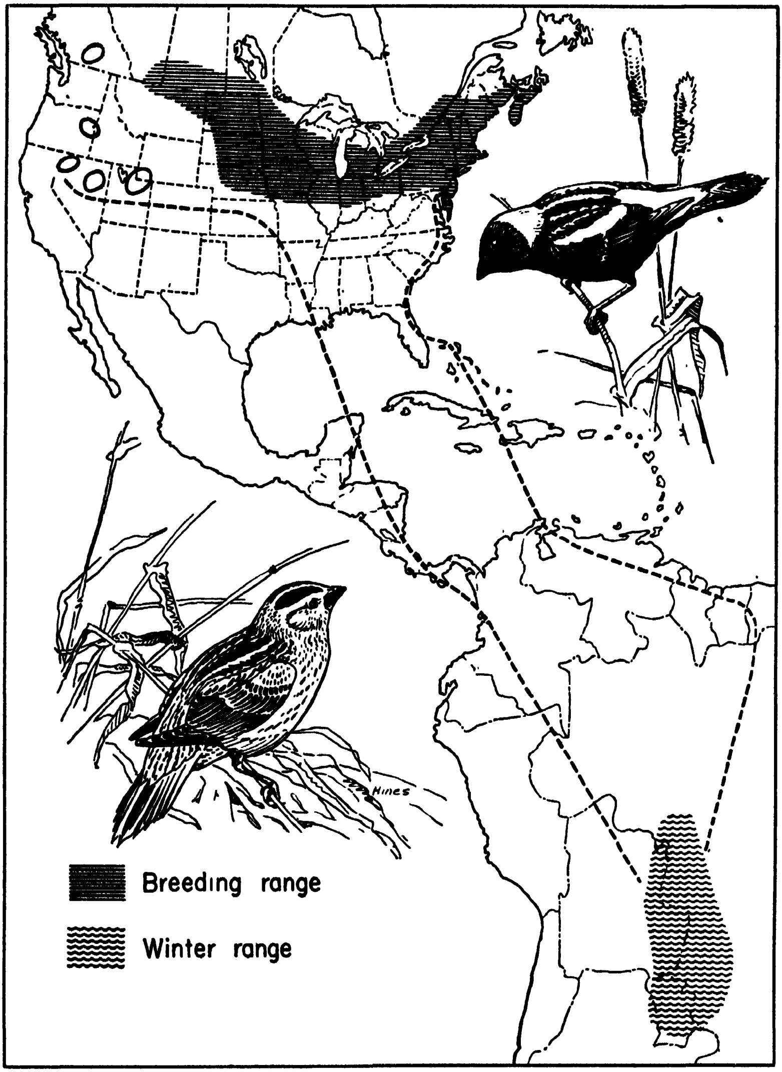

Fig. 16·12. *Distribution and migration of the Bobolink. It is assumed that birds in the western colonies, established since the coming of the white man (circles on the map), migrate east and south rather than by taking the short cut through Mexico. (From Frederick C. Lincoln,* Migration of Birds, *U. S. Department of the Interior, Fish and Wildlife Service, Circular No. 16, p. 56.)*

respective ranges are influenced by *tradition*. Because the families stay together, those that know the way are accompanied by young unfamiliar with the route and range, so that over the years a fixity of route may result. This influence of tradition may explain the shift reported in the Snow Goose route in 1884 from the eastern to western shores of Hudson and James Bays. Wind is said to have forced the Geese across James Bay, and the route is still followed.

In Europe, the general direction of migration is to the south and southwest, though some birds move in a south-easterly direction into southern Asia. Some have also been reported migrating nearly east-west. Birds of adjoining continental areas often pass into the British Isles. Birds of Europe that winter beyond its borders tend to cross into Africa, some to South Africa. The migration in Asia is less known, but it seems to be south and southeastward into adjoining islands and the lands of the Pacific, or southwestward into Europe and Africa. Some species may reach Australia, while many winter in Asia Minor or pass on into Africa.

A few birds from Alaska cross into Asia to winter, just as the Arctic Tern may cross to the east side of the Atlantic (Fig. 16·9).

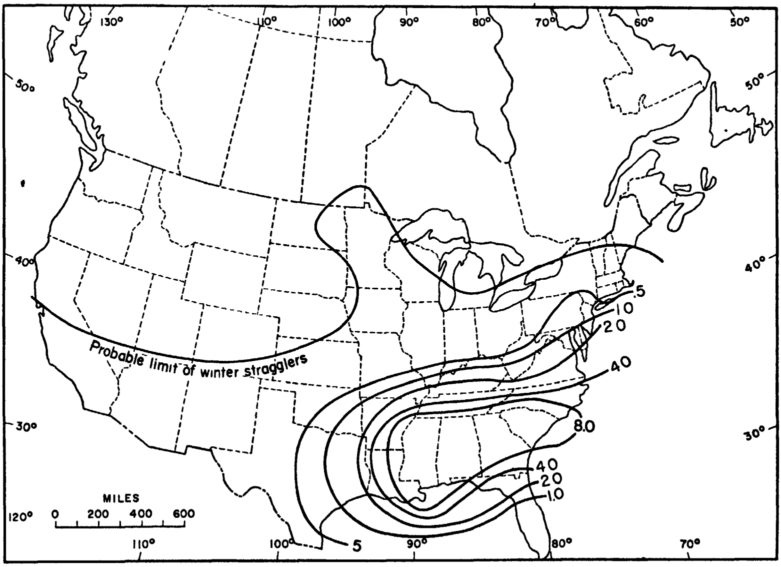

Fig. 16·13. *The White-throated Sparrow appears in the West only as a straggler. In winter, its zone of concentration lies in the Southeast. The isopleth lines indicate average birds reported per hour of censusing during the Audubon Christmas Census, 1900–1939.*

These are explained as migration routes that retrace the ancestral path by which the species spread.

Concentration Areas. Birds may winter over a great area but concentrate in only part of it where conditions are most favorable. The White-crowned Sparrow winters over much of the United States, but its winter distribution shows a concentration area in the West. The White-throated Sparrow appears in the West as a straggler and has a concentration area in the Southeast (Fig. 16·13). The Tree Sparrow winters over much of the United States and Southern Canada, but its concentration area lies in the mid-south. The American and Red-breasted Mergansers winter wherever open water can be found. But the Red-breasted is more coastal and its concentration area not so far northward.

The migrations of a few North American birds illustate the relationship of summer and winter range. The Harris Sparrow breeds in northern Canada and winters in the south-central region from Nebraska to Texas. Fall stragglers, largely young, may wander west to California or east to Ohio. The subspecies of the Fox Sparrow along the coast of western North America have long been noted for their use of "leap-frog" winter range. The races living farthest north winter farthest south and other races winter in between.

SUGGESTED READING

ALLEE, W. C., ALFRED E. EMERSON, ORLANDO PARK, THOMAS PARK, and KARL P. SCHMIDT, *Principles of Animal Ecology.* Philadelphia: W. B. Saunders Co., 1949.

*ALLEN, ARTHUR A., *The Book of Bird Life.* New York: D. Van Nostrand Co., Inc., 1930.

*ALLEN, GLOVER M., *Birds and Their Attributes.* Francetown, N. H.: Marshall Jones Co., 1925.

*ARMSTRONG, EDWARD A., *Bird Life.* New York: Oxford University Press, 1950.

CLARKE, WILLIAM EAGLE, *Studies in Bird Migration,* 2 vols. London: Gurney & Jackson, 1912.

*GRISCOM, LUDLOW, *Modern Bird Study.* Cambridge, Mass.: Harvard University Press, 1945.

HEAPE, WALTER, *Emigration, Migration, and Nomadism.* Cambridge, England: W. Heffer & Sons, Ltd., 1932.

*LINCOLN, FREDERICK C., *The Migration of American Birds.* New York: Doubleday, Doran & Co., 1939.

LINCOLN, FREDERICK C., *Migration of Birds.* U. S. Department of the Interior, Fish and Wildlife Service, Circular No. 16, 1950.

MATTHEWS, G. V. T., *Bird Navigation.* Cambridge, England: Cambridge University Press, 1955.

PEARSE, A. A., *Animal Ecology.* New York: McGraw-Hill Book Co., Inc., 1939.

*THOMSON, A. LANDSBOROUGH, *Bird Migration.* London, England: H. F. & G. Witherby, Ltd., 1936.

WETMORE, ALEXANDER, *The Migration of Birds.* Cambridge, Mass.: Harvard University Press, 1927.

SIMMS, ERIC, *Bird Migrants.* London: Cleaver-Hume Press Ltd., 1952.

17

Bird Song

Rivaling bird flight as the most distinctive single characteristic of bird life, bird song reaches a state of perfection altogether unknown among any group of animals. It is, paradoxically, one of the least studied attributes. No invertebrate group or other vertebrate group has song so widely used and so well developed. Because birds possess the very great mobility that flight confers, sound, with its high speed of transmission, seems a better mode of communication than scent, which is slow. Animals of low mobility find scent suitable, either alone or in conjunction with modest vocal powers.

Among the vertebrates man alone seems to have a musical discrimination at all like that of birds. The reasons may be the same, chiefly that both man (with a poor sense of smell) and birds depend mostly upon sight and sound for detecting friends and foe alike, or for judging the state of the environment. The fact that birds use musical elements similar to those of human music suggests that (a) one learned from the other, (b) both accidentally struck upon the same pattern, or (c) music as we know it is a deep-seated, biological attribute. Because some frogs and some mammals also use musical notes as of the "human" musical scale, an ancient origin of music in animal history is indicated.

Studies show that from the psychological standpoint, the ear receives and becomes aware of *patterned sound* more easily than unpatterned sound. It is not clear, however, whether patterned sounds have greater radiating power than unpatterned ones or whether they may be produced more easily. Yet the evidence that sounds may be received and understood more easily when patterned indicates that communication (as measured by the effort at reception on the part of hearers) in turn is more efficient when effected by patterned sound. Music is patterned sound, and its adoption becomes more understand-able against the background of the struggle for use of biological energy. It indicates quite clearly that music is yet another animal characteristic of an adaptive nature.

Birds produce vocal sounds in the *syrinx*, a structure peculiar to them, whereas mammals produce vocal sounds in the *larynx*. The mammalian voice box—with which so many people gain familiarity through use—consists of a cartilaginous enlargement at the *upper* end of the trachea termed the *larynx* (and commonly called the "Adam's apple"). This structure contains vocal cords, thin bands of fiber sheathed in a mucous membrane. The tension and placement may be altered by means of muscles. At will, the column of air passing across the vocal cords, usually during exhalation, causes them to move and to generate audible vibrations. Birds, on the other hand, possess no functional larynx. The *syrinx* is situated, not at the upper end of the trachea as in mammals, but at the *lower* end of the trachea.

VOICE EQUIPMENT

Syrinx: The Voice Box of Birds. Birds have three kinds of syrinxes (also spelled syringes): *tracheal*, *bronchial*, and *tracheobronchial* (Fig. 17·1), all of which bear a general similarity. Some anatomists distinguish only the second and third types; confusion apparently stems from the fact that some anatomists consider certain elements as split tracheal which others consider as split bronchial rings. The syrinx demonstrates yet again the tendency of bird evolution to transfer weight to the body interior. If a muscular larynx were at the

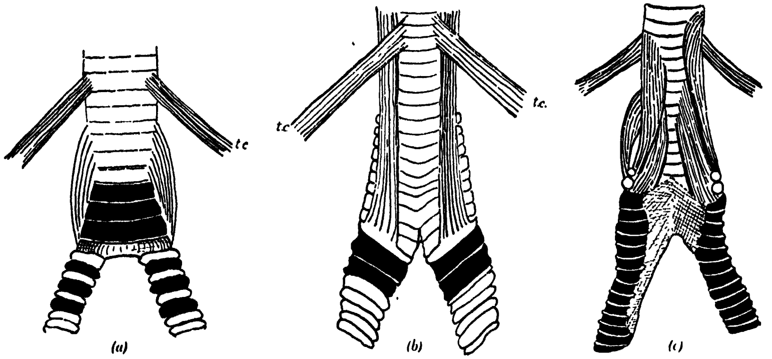

Fig. 17·1. *Three kinds of syrinxes: (a) Tracheal, (b) bronchial, and (c) tracheobronchial; t.c., tracheoclavicular muscle. (After Alfred Newton,* A Dictionary of Birds, *p. 940. London: Adam & Charles Black, 1893–1896.)*

upper tracheal end, for example, its weight and that of associated tissues would be brought ahead of the wings. The syrinx at the lower end brings weight near the body center and under the supporting wings. The long trachea carrying sound also offers possibilities for voice modification not otherwise so easily obtained.

The tracheobronchial syrinx (the most common kind), includes modifications of the two bronchi and tracheae, as the name implies. The anterior bronchial rings are incomplete on the dorsal side, leaving a gap closed by the *tympanic membrane.* The *pessulus* extends across the bronchial rings and is covered by the *semilunar membrane.* The sounds are produced by vibration of the tympaniform membranes in many and perhaps in all birds. In the bird (at least in the Passerines) it appears that air passing *outward* (i.e., exhalation) makes all sounds (Miskimen, 1951). *Intrinsic* and *extrinsic muscles* (of the interior and exterior of the syrinx) control the shape and tension of the chamber, pessulus, and semilunar membranes to produce variations of sound. The tenth and twelfth cranial nerves innervate these muscles (page 74).

The tracheal syrinx resembles the tracheobronchial syrinx in construction but involves only the trachea, and even then only its lower part. It occurs in Wood-hewers and Ant-thrushes of South America and perhaps also is the type found in Storks.

The bronchial syrinx is formed of incomplete rings and loose membranes in the bronchi somewhat similar to those of the tracheobronchial syrinx. The passage of air sets up vibrations in the loose membranes between the bronchial rings. This type of syrinx occurs in some and perhaps in all members of the Cuckoo, Goatsucker, and Owl families.

The general make-up of the syrinx thus consists of (a) the supporting framework, (b) vibratory internal membranes of several types, (c) muscles for controlling the membranes and syrinx, and (d) nerves for controlling the muscles. Singing ability depends upon muscle and nerve abundance, as well as upon the excellence of coordination. It reaches its highest state in the Passerines, which may have five to seven pairs of syringeal muscles. The vibrations of the syringeal membranes set up vibrations in the column of air. The length of the trachea seems to influence the tone largely by acting as a resonator or modifier.

Modifications and Accessory Organs. Some birds have modifications of the vocal organs or have accessory organs for controlling or assisting in the production of sounds characteristic of the species. Both the Trumpeter and Whistling Swans, for example, have greatly lengthened windpipes (tracheae) for modifying or amplifying the tone, somewhat as does a trumpet. These windpipes actually invade the sternums. The trachea of the Whistling Swan has a simple extra convolution, but the Trumpeter Swan not only has an extra convolution but also a dorsal bend in the windpipe that fills a projection from the sternum into the body cavity.

The Whooping and Sandhill Cranes have tracheae likewise entering the hollow keel of the enlarged sternums. The enlargement in the Whooping Crane includes some 27 inches of the coiled trachea, itself about 50 inches long and actually longer than the body of the bird. The extra convolution of the Sandhill Crane windpipe is but 8 inches compared to 27 inches for the Whooping Crane. The respective names of Whooping Crane, Whistling Swan, and Trumpeter Swan reflect the differing voices associated with the differing tracheal convolutions (Fig. 17·2).

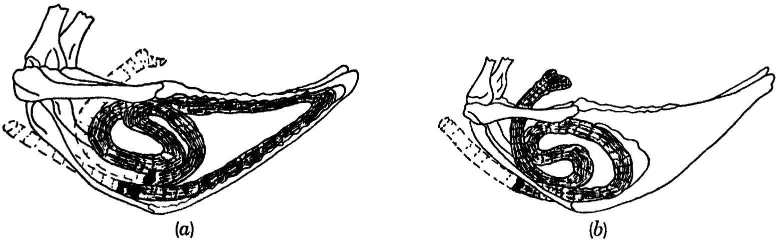

Fig. 17·2. *Coiling of the tracheae of the Whooping Crane (a) and Sandhill Crane (b) in the sternums. The tracheae actually coil in a somewhat spiral direction so that parts of the loops in these views are behind others. (After Elliott Coues,* Key to North American Birds, *p. 209. Boston: Dana Estes Co., 1903.)*

Paired *resonating chambers* are common among members of the Tetraonidae. In the male Sage Grouse of the American sagebrush country, the lateral walls of the esophagus can be distended by muscles having their origins in the bony framework of the neck and their insertions in the esophagus. The performing bird apparently closes the trachea at the glottis (possibly the nostrils also), and pumps air from the lungs into the distensible pouches. Careful field observation indicates their capacity, for it requires three intakes of air exhaled into the esophagus to fill them (Scott, 1942). At the conclusion of the picturesque display, the sudden collapse of the pouch and escape of air makes a resounding PLOP, reportedly as the sides of the pouches meet.

Resonating chambers are found also in the Prairie Chicken, Sharp-tailed Grouse, Black Grouse, Capercailie, Spruce Grouse, Franklin Grouse, and Blue Grouse (Figs. 17·3, 17·4). These evidently func-

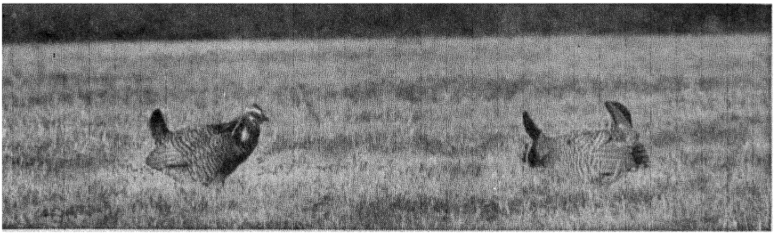

Fig. 17•3. *The inflated resonating chambers of the Prairie Chicken show in the "booming" bird at the right and the one pausing at the left. The feathers of the throat open to reveal the bright yellow pouches. (Photograph by Staber W. Reese. By permission of the Wisconsin Conservation Department.)*

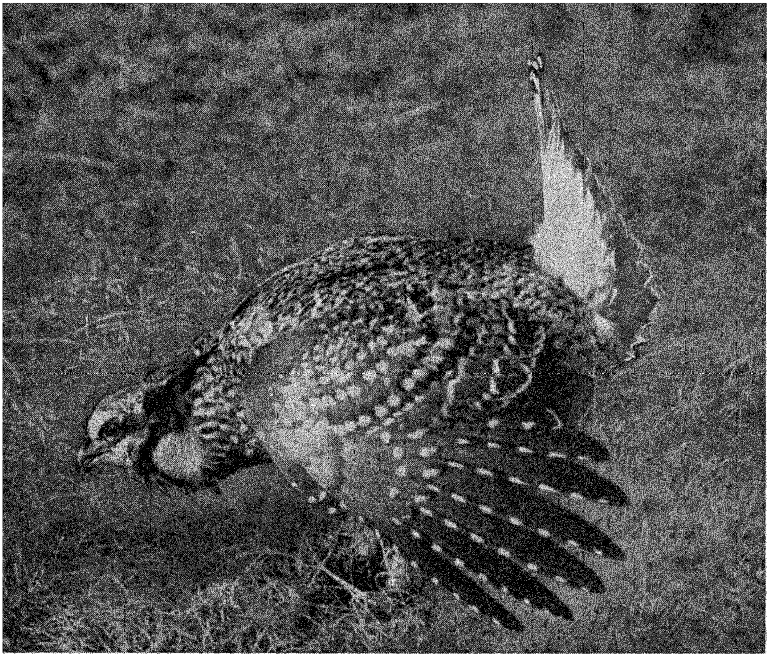

Fig. 17•4. *The courtship of the Sharp-tailed Grouse includes dancing. Vocal cluckings are part of the performance, during which the neck pouches are inflated. (Photograph by Staber W. Reese. By permission of the Wisconsin Conservation Department.)*

tion to build up resonance. It may be that the actual passage of air across the opening of the pouches produces the sound or adds resonance. The Emu has an air pouch also, a single one opening off the lower side of the windpipe at a point where the rings are incomplete.

SOUNDS AND THEIR USE

Instrumental Calls and Songs. Some birds have nonvocal or "instrumental" calls and songs either replacing vocal ones or adding to them, but most birds using "instrumental" calls or songs have rather low vocal ability. There are five general ways of producing nonvocal sounds; these involve (a) escape of air, (b) use of feet, (c) use of wings, (d) use of tail, and (e) use of bill. It has been said that all instrumental sounds of an orchestra have their counterparts in various bird sounds (Armstrong, 1947).

The PLOP! made by collapse of the air pouches in the Sage Grouse has already been mentioned. The Ostrich and some Geese produce hissing sounds by the passage of air through the mouth. Even the Black-capped Chickadee incubating in its nest hole will give an explosive hiss at an intruder.

A few birds produce sounds by stamping their feet in a dance. Prairie Chickens dance in this way during the courtship performance as a prelude to *booming*, but their stamping makes a rather weak sound heard only a short distance. It is subordinate to the booming proper (Fig. 17·3). A near relative and associate, the Sharp-tailed Grouse, depends largely upon its feet for making sounds in courtship. (But some observers have suggested that the sound results from rattling of the wing or tail feathers). The males stamp their feet with great rapidity and seem to "float over the ground like drops of water on a hot stove," meanwhile producing loud sounds having the rhythm and likeness of those from an air drill or riveting hammer (Fig. 17·4).

The male Ruffed Grouse mounts a log or other platform and drums with his wings; he produces sound by the quick snap of his wings against the air (Fig. 17·5). The common barnyard rooster also produces a flapping sound by drumming with his wings; even a male Ring-necked Pheasant on his crowing grounds drums with his wings. *Drumming flight* occurs among several members of the Grouse family. The Blue Grouse, for example, rises a short distance into the air and drums rapidly with his wings as he rises (about 3 feet off the ground) and descends (Wing, 1946a).

The peculiarly constructed outermost primary feathers of the Woodcock make a whistling sound in flight. The birds feed and

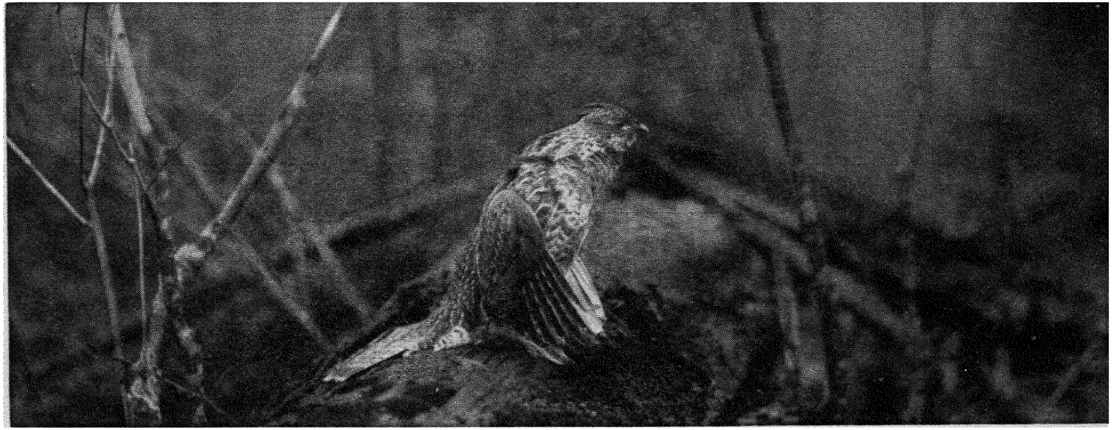

Fig. 17·5. *The Ruffed Grouse drums with the wings as part of his courtship performance. This picture was taken from a blind built across an end of the drumming log. (Photograph by Franklin J. W. Schmidt. By permission of the Wisconsin Conservation Department.)*

fly much at night and the whistling of the wings may be both a warning sound and a position marker. If the outermost primary of each wing is clipped, the whistling sound will not be produced. The tail feathers of the Anhinga have a "fluting" that gives them a washboard look; the fluting at times makes a rippling sound as the bird moves through the air. The *winnowing* of the Snipe as it circles over the marsh is caused by air vibrating the outer tail feathers especially developed for this purpose (Fig. 17·6). The Manakin of the Neotropical region makes a rattle with its peculiar wing feathers as it jumps back and forth through the air. Only the male has these special feathers (Fig. 17·7).

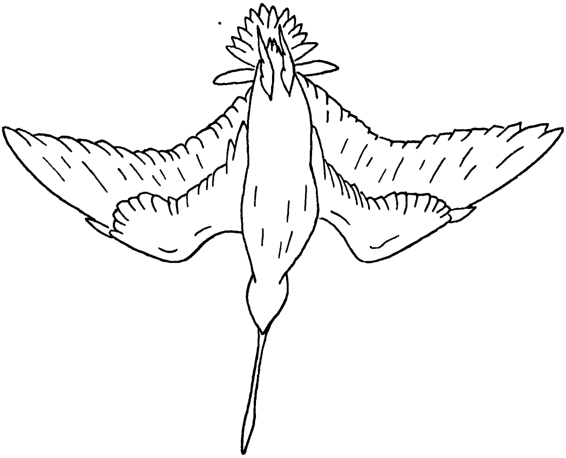

Fig. 17·6. *The characteristic position of the Snipe and its tail in making its "bleating" sounds during flight. (After P. H. Bahr, "On the 'Bleating' or 'Drumming' of the Snipe* (Gallinago coelestis)," Proceedings of the Zoological Society of London *(1907):12–35.)*

Function of Songs and Calls. There seem to be three general functions of calls and songs in the bird world: *communication, advertisement,* and *identification.* Advertisement and identification perhaps are merely forms of communication, so that fundamentally sounds have but a single function (unless they serve for the satisfaction of the bird itself or as outlets for the emotions, as has been suggested in regard to some bird songs).

A simple example of communication is the call of a lost chick and the hen's clucking response in the farmyard. But communication calls need not be directed, for the call of the same lost chick seized by a

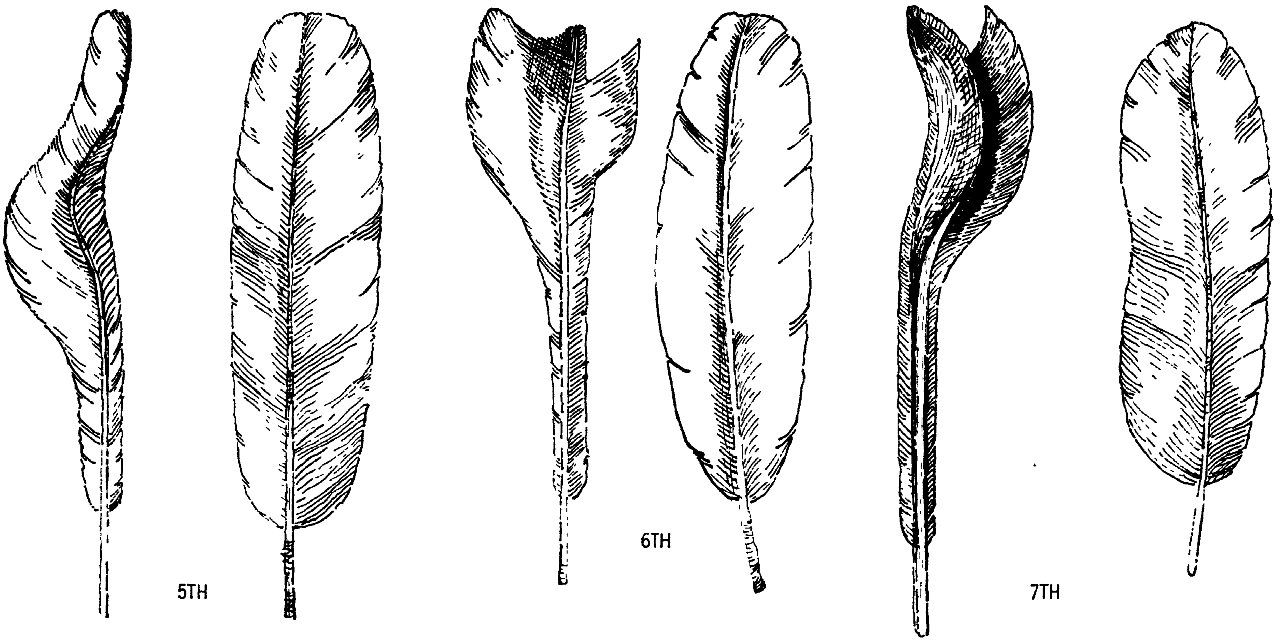

Fig. 17·7. *Fifth, sixth, and seventh primaries of the Manakin to show the special development in the male (left feather of each pair) in contrast to the usual feather as found in the female (right feather of each pair). Fifth and sixth are top views, the seventh a view from the under side. (After Alfred Newton,* A Dictionary of Birds, *p. 533. London: Adam & Charles Black, 1893–1896.)*

person or enemy is a cry of fear or alarm understood by the bird world in general, even though the mother herself is the one most likely to respond. Many species recognize the hunger call of young birds not of their own kind.

Calls between members of a mated pair (e.g., Fig. 19·5), such as during interchange of incubating birds, may be identification calls; they may also signal readiness to change places; and they may be part of a complicated behavior pattern. Birds that flock have calls that serve to keep the flock in contact; thus, the continuous twitter of the Slate-colored Juncos in a flock seems to aid materially in maintaining the flock continuity. Lost or detached members of a flock are guided back by the flock calls as well as by responses to their own "lost-bird" call notes. Flock calls and twitters not only serve to maintain flock continuity but may serve also as *sequestration notes* that maintain distance between the various members within the flock.

The *warning call* of the American Robin or Song Sparrow whether given in the flock or when a bird is alone, is recognized by other Robins and Song Sparrows and many other species as well.

Vocal sounds often serve as an important activity and behavior regulator of Black-capped Chickadees, especially in the flocking season. The use of sounds made by this species has been particularly well explored. It is known that at least sixteen different calls and notes are used, eight of which function primarily during breeding behavior and eight primarily in general social relations, as follows (Odum 1941–1942): "Phoebe" song, signal song, alarm note, recognition note contact note, flight or restless note, warning note, dominance note musical "to-will," begging note, mating (?) note, "perplexed" note "hissing" or "bluff" note, distress call. Comparable studies of other species may show similar "language."

Sounds may have several functions at various times (Armstrong 1947). They may serve to:

1. Identify the singer to its own or other species
2. Place-mark the bird and its territorial holdings
3. Indicate the vigor and dominance of the singer
4. Indicate the stage of the singer in the breeding cycle
5. Indicate location of the bird in relation to communal roost
6. Induce another bird to disclose its sex
7. Attract the sexes and influence sexual behavior
8. Intimidate and drive off intruders
9. Provide signal for activity change, as at the nest

The very great individual variation in songs so characteristic o some species suggests a functional purpose. But of this we are ignorant. The variation among Song Sparrows and Eastern Meadowlarks for example, may indicate that they have a greater need for individual recognition or identification by ear than do birds that sing the same few notes over and over as in the Black-capped Chickadee. But there may be variations of quality or expression in the seemingly simple songs that accomplish much the same thing.

Singing Position. Birds tend to sing from conspicuous perches, even though customarily they may inhabit the interior of bushes or dwell on the ground. Birds normally inconspicuous or retiring, like the Grasshopper Sparrow, may mount to an exposed perch at the top of a tree, bush, or weed to sing. Some ground-nesting birds, like the Savannah Sparrow and Meadowlark, ascend low natural perches and fence posts if available. Several Vireos have the interesting habit of singing while on the nest.

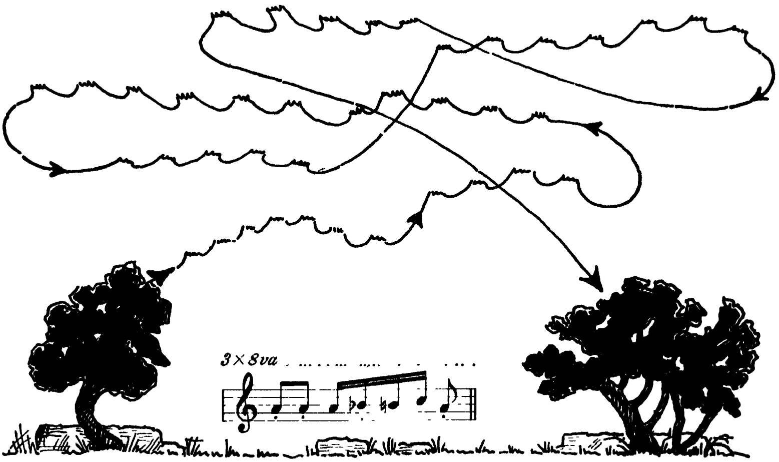

Fig. 17 • 8. *Flight song of the Vermilion Flycatcher. The bird hovered in air while singing the song, shown by its musical notes, at each wavy place in the line tracing the flight path. Arrows indicate the direction of flight and final dive into a red cedar tree. The song was repeated thirty-nine times before alighting. (Drawn from life by Anne Hinshaw Wing, at Junction, Texas, June 30, 1950.)*

It would seem to be an easy step from using an open song-perch to singing on the wing (page 283). The Skylark of the Old World has long been known for this habit, but many birds in the New World do likewise. Actually, flight song is a somewhat characteristic habit among birds of the grassland, prairie, desert, and marsh where perches are few. Some of these birds have been called *lark* in recognition of singing flight. Among the best known birds engaging in singing flight are the Snipe, Nighthawk, Ptarmigan, Pipit, Vermilion Flycatcher, Scissor-tailed Flycatcher, Chat, Lazuli Bunting, Horned Lark, Lark Bunting, Meadowlark, Bobolink, and American Marsh Harrier of the open fields, grasslands, pastures, or marshes (Fig. 17·8). Yet some birds of brush and woodland engage in singing flight at times, occasionally over the forest canopy, and sometimes often enough for it to be called a subordinate habit. The Ovenbird and Boat-tailed Grackle, for example, sing in flight even though this is not so pronounced nor so spectacular a habit as in birds of the grassland like the Lark Bunting. Many birds like the Mockingbird, Painted Bunting, and House Finch may continue singing during flight from one perch to another, but their songs may or may not be true flight songs. In other parts of the world, flight song occurs also. Among the examples may be listed the Whitethroat, Tree Pipit, Rock Pipit, Glossy Grassquit, King Bird-of-paradise, Pratincole, Greenshank, Lyre-tailed Honey Guide, Dunlin, and Black Penelope (see also Courtship Performances, Chapter 18).

Calls of Adult and Young. Males do most of the singing during the breeding season, and the syrinx of the male often shows a greater development than that of the female. Some immature male birds may sing, but usually only the mature males do so. The first-year bird's song may be less complete than that of the older male at the start, which suggests the need for practice or listening to others and probably also for further physical and nervous development. Some birds still wearing immature plumage may sing about as well as the adults; this is especially noticeable in the American Redstart, Purple Finch, House Finch, Painted Bunting, and Red Crossbill. These species, however, may take more than one season to acquire the fully adult plumage.

Because singing by males is so apparent, singing by females has been generally overlooked; yet females of some fifty-six species are known to sing (Nice, 1937, 1943). Call notes of females generally are the same as those of the males, although as in man, the voice of the female may perhaps be softer and higher pitched. The Horned Owl and other Owls show this characteristic, which may indicate a trait of the order (Miller, 1934). The call of the female may vary in tone quality and loudness in the Mallard Duck and other dabblers. The males of Dabbling Ducks have a softness of voice produced by a muting device in the syrinx, which itself is actually larger and better developed than that of the loud-voiced female. The singing of females may be (a) rather indiscriminate calls associated with the song of the male, (b) antiphonal response to the song of the male, (c) sounds fitting into those of the male to make a "joint song," or (d) sounds independent of any by the male.

Bob-white young hatched in an incubator will sing the typical "Bob-white!" when adult, although they have never heard any such song before. But the young of species having more complicated songs, like the Meadowlarks, native Sparrows, and others, may possibly have to learn the finer points of their song by hearing others sing it, though of this subject little is known. The first hearing of the adult song may release a pent-up channeling of impulses, so that from then on the true song will be sung as in the species. Some ornithologists have suggested that among some species the male sings near the nest during the late stages of nesting so that the young can hear the song of the species, the memory of which it retains until it becomes an adult, or may even reinforce by singing when it is still an immature bird. The evidence for the development of song and its relation to instinct and association is rather meager (Thorpe, 1951).

TIME AND FREQUENCY OF SINGING

Songs and Seasons. Bird song reaches its highest state of perfection during the peak of the breeding season. Early singing occurs on warm days in cool regions. Temperatures lower than 50° F. inhibited Song Sparrow singing in mid-January; by mid-February, the inhibiting limit had dropped to about 28° F. (Nice, 1937). Early songs in northern latitudes may show incompleteness. In mixed flocks of Prairie and Northern Horned Larks found together in the same field, the Northern Horned Larks can be differentiated by their song, which has only its first few notes whereas the song of the Prairie Horned Lark is then the complete or nearly complete song characteristic of the species. Later in the season, Northern Horned Larks will also sing the complete song. Early songs usually occur first on warm spring days; however, some birds may sing on sunny days in midwinter.

The autumn recurrence of drumming in the Ruffed Grouse has been termed *fall recrudescence.* It may be a premature expression from an early hatched bird or perhaps a contrastimulation from gonadal refraction. Snatches of song also occur among early hatched birds but the renditions are usually incomplete. Other premature acts of immature birds such as nest construction and northward fall movement (page 302) have been reported. The significance of the fall recrudescence, however, has not been determined.

Length of Singing Seasons. Singing declines rather slowly with the passing of the height of the breeding season in mid-latitudes but

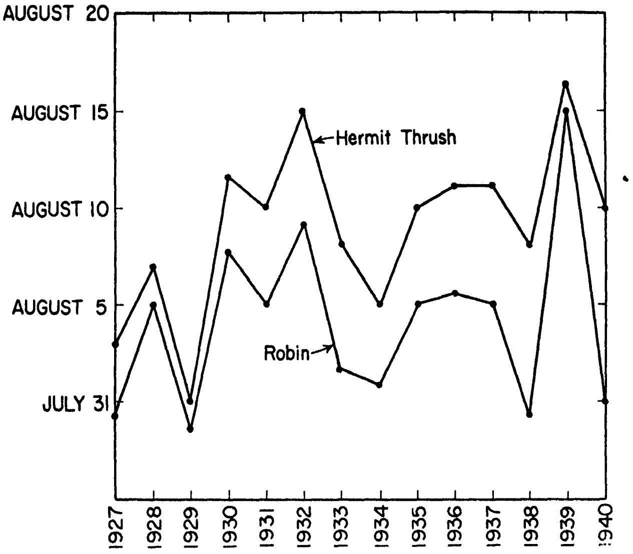

Fig. 17·9. *A 14-year record of the cessation of song by the Hermit Thrush and American Robin. (After Aretas A. Saunders, "The Seasons of Bird Song: The Cessation of Song After the Nesting Season,"* Auk, *65(1948):19–30.)*

Table 17·1
Song Order and Season for Ten Species in Arkansas

Species		Spring Rank (Beginning Song)	Fall Rank (Ending Song)	Length of Season (Days)
Mourning Dove	March 1–September 1	2	5	135
Eastern Phoebe	March 10–October 1	3	9	205
Wood Pewee	May 1–September 10	9	7	134
Bell Vireo	May 5–September 5	10	6	124
Yellow-throated Vireo ...	April 10–September 15	6	8	159
Black and White Warbler .	April 1–July 25	5	2	116
Yellow Warbler	April 18–July 10	8	1	83
Yellow-throated Warbler..	April 15–August 10	7	3	118
American Goldfinch	March 20–October 20	4	10	215
Red-eyed Towhee	February 10–August 15	1	4	187

Source: W. J. Baerg, "The Song Period of Northwest Arkansas," *Auk*, 47(1930): 32–40.

with dramatic suddenness in the Arctic regions where daylight declines rapidly after midsummer. In the Northland, song comes to a rather abrupt end in a matter of days, whereas it may take weeks farther south. The cessation of song in summer and fall is less uniform in mid-latitudes than is the beginning of song in spring. There may be a month or more of difference between the dates of ending in successive years. Part of this may result from difficulties that observers are bound to have recording the exact date of last song. Some confusion may result from the fall singing of immature birds, such as the immature Yellow-throated Vireos that may sing well before the fall migration (Sutton, 1949). Fig. 17·9 shows a 14-year record of song cessation. Table 17·1 gives examples of the song periods for ten species and shows the order of spring song-start and fall cessation as well as length of song season.

Hours of Singing. Among diurnal birds, singing during the height of the breeding season reaches its peak in the morning. As a general rule, singing begins near dawn and rises to a peak a few hours after sunrise, followed by a lull during the middle of the day and a resumption toward evening (see Fig. 11·5). It thus parallels the daily activity rhythm (page 213). Early in the season, song may be rather uniformly distributed throughout the day, but as the season progresses, singing occurs chiefly in the early morning and evening. Midday singing occurs regularly early in the season but later only on cool or cloudy days; in fact, there is a marked resumption of singing on cloudy days. Even the passing of a heavy cloud (or eclipse) may bring outbursts of song in the American Robin. Birds are attuned to light conditions, the amount of light being relative (see Chapters 11 and 16). Late in the season, birds sing only in the early morning or late evening hours and stop during the heat of the day, although there are exceptions, such as the Warbling and Red-eyed Vireos, that sing more or less continuously even in midsummer.

Nocturnal and crepuscular birds, like the Screech Owl and Whip-poor-will, sing in dusk and darkness; they rarely sing at all during the day except when it is cloudy. Yet some diurnal birds may sing at night. The Mockingbird is especially likely to sing on moonlight nights and often on dark nights as well. The Ruffed Grouse may start drumming early in the morning, several hours before daylight, and may even drum irregularly at other hours during the night. In the high latitudes, some birds sing many hours a day. The Gambel Sparrows, for example, stop all singing during only an hour or so in the Arctic night—a twilight sometimes in actuality. The Gambel Sparrows may sing at intervals during about 22 hours of the 24; when they sleep is not quite clear.

Repetition of Song. Songs vary widely from the short, simple, single note of the Pygmy Owl, for example, to the long complex series of musical notes of the Winter Wren. It is said that, in general, the shorter the song, the greater the likelihood of its immediate repetition, and that the longer songs come at longer intervals. But there are many exceptions; the Pygmy Owl sings at rather long intervals, longer than those of the Winter Wren. Because sound as a means of communication does not linger long (compared to the lasting qualities of scent used by animals which use the nose for gathering messages) the need for repetition of song seems real and practical. It is reported also that a *monotony threshold* exists. Singing of repetitious songs usually is discontinuous (e.g., Prothonotary Warbler); continuous singing usually is versatile (e.g., Thrushes) (Hartshorne, 1956).

A Chuck-will's-widow sang, by actual count (Johnson City, Texas, June 28, 1950), at the rate of 27 songs per minute at 9:20 P.M. and of 23 per minute at 4:25 A.M. the next morning. As these two periods are at the peaks of diel activity for a nocturnal bird, even with half as much singing during the "lull" period the bird would have sung 10,000 times a night. Its 100 days of singing would suggest a million songs, even though the count indicated was near the end of the song season. The song of the Chuck-will's-widow has a regular five-note length not counting the opening *chuck*. The song of the Whip-poor-will has three notes (others may be heard sometimes at close quarters) and it has been estimated to sing at the rate of 58 to 63 songs a minute. The song of the diurnal Chipping Sparrow, on the other hand, has from 10 to 18 notes. A careful count indicates that 12 to 15 notes with an average of 13 is usual. The number of songs averages 5.5 per minute during the peak of singing. Presumably no fewer than 200,000 songs would be sung in the 150-day season, and probably a figure twice that would be more nearly representative. Its relative, the Clay-colored Sparrow, sings 7 to 10 times a minute.

The Blue Grouse sings ("hoots") a series of 4 to 6 notes, but fully 90 per cent of its songs contain 5 notes. More than 50,000 songs may be sung during the season. The Ruffed Grouse may drum 10,000 or more times in the spring. But the Bob-white whistles only during bachelorhood; one favored by early mating might whistle as few as 100 times in a season. An American Redstart sang intermittently at a rate of 14 songs a minute. It seems probable, however, that among diurnal North American singers, the Red-eyed Vireo (35–41 phrases a minute) or one of its fellow Vireos may hold the record for the greatest singing effort during the season. They sing rather regularly, even during the middle of the hot summer days when all else is still, almost to the end of the song season. In its 130–135 days of singing, a Red-eyed Vireo may sing two to three million phrases ("songs").

A faithful ornithologist counted *all* the songs sung by a male Song Sparrow, which totaled 2,305 on the day of counting, May 11. The bird averaged 242 per hour in the morning and 150 in the afternoon (Nice, 1937). His top speed of singing seems to have been at the rate of about 5 a minute. Other reported song *rates*, converted to an hourly basis, follow: Red-eyed Vireo, 2,200; Eastern Phoebe, 2,100; Black-headed Grosbeak, 1,300; Clay-colored Sparrow, 480; Song Sparrow, 300; Chipping Sparrow, 330; and Prothonotary Warbler, 300-360.

STRUCTURE OF SONG

Physics of Bird Song. Like all other sounds, bird song consists of sound *vibrations* known as *frequencies*. The more rapid the frequency, the higher the *pitch*, and the higher the pitch, the higher the song sounds to the ear. Man hears from a low of about 16 vibrations a second to a high of about 18,000, but the hearing range and its completeness vary with individuals and with age. No doubt psychological reactions as well as training and practice enter into hearing ability. Bird hearing may reach (after conditioning) as high as that of man but only as low as 50 (Schwartzkopf, 1955). It is suggested that opening of the mouth by the bird may interfere with its own hearing through tension on the ear drum; this does not seem to be so in mammals (Bray and Thurlow, 1942).

The hearing range of birds and mammals in general appears to vary somewhat with the range of the voice so that the latter roughly indicates the expected relative hearing range. A bird with a high voice appears to have a hearing range higher than that of a low voiced bird. But it must be remembered that measurements indicate the range in terms of *pure tones*, which rarely occur in animal voices. A bird like the Starling, for example, that probably hears no pure tones below 700 vibrations a second could hear the hoot of a Horned Owl at 256 vibrations a second because of *overtones*. In the same way, a Warbler that would not hear the ordinary speech of man if given in pure tones could perhaps be aware of a conversation under his perch because of these same overtones. It seems to be a workable generalization that birds hear and recognize instinctively the sounds of their enemies (e.g., a Crow hears the hoot of a Horned Owl) on the one hand, and the sounds of their prey on the other (e.g., a Screech Owl hears the squeak of a mouse). The highest sensitivity is in range of a bird's own voice; among exceptions are Owls whose highest sensitivity is in range of mouse squeaks (Schwartzkopf, 1955). The hearing ranges of several birds have been determined (Table 17·2).

Table 17·2

Hearing Ranges Determined for Several Species

Species	Frequency (Vibrations per Second)
Canvasback	190– 5,200
Great-horned Owl	60– 7,000
Rock Dove	200– 7,600
Horned Lark	350– 7,600
Starling	700–15,000
House Sparrow	675–11,500
Snow Bunting	400– 7,200

A sound heard by the ear as a single note may upon analysis prove to be several notes given rapidly (Brand, 1938). The Song Sparrow song lasting 2 to 2½ seconds may have as many as 35 or 36 notes given at the rate of 15 to 17 a second. These notes of one-fiftieth of a second in duration are followed by a pause of a two-hundredth of a second, and so on. There may be rapid changes of pitch as well, too rapid for the human ear to detect. One or more notes sometimes may be started before another has ended. Perhaps such changes may be heard as a double tone or multiple tone whose pitch is difficult to determine. The average human ear is unable to separate rapid notes from one another. Similarly, the eye recognizes the sixteen or more pictures cast on the screen each second by the motion-picture projector as a continuous scene. Yet we know that it is not continuous. Audiospectograph analyses of bird songs, e.g., Carolina Wren (Borror, 1956), show that the song pattern consists of a number of short phrases. Presumably these are the "building blocks" of which bird songs are made. The ability to determine *time* and *pitch* varies in man * and probably in individual birds also.

The average frequency reported for Passerines is about 4,280 vibrations per second, which is above that produced by the violin and piano but within the range of the piccolo. The average frequency is highest among Warblers and may be a full octave above the piano. Sound engineers say that birds follow the general rule that the smaller the instrument, the higher the sounds produced. A frequency of

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* An ornithologist who recorded his inability to hear bird songs as he advanced in years found that he could no longer hear the Golden-crowned Kinglet and Brown Creeper after he reached 60, Cedar Waxwing after 65, and Black and White Warbler after 67 (Saunders, 1934).

12,225 vibrations per second has been reported for the Black-poll Warbler and 9,500 for the Grasshopper Sparrow (Brand, 1938). But whether or not microphones faithfully pick up the highest notes of birds remains to be seen. A sample of the frequency range reported for some birds appears in Table 17·3. How birds achieve pitch discrimination is a mystery (Schwartzkopf, 1955).

Table 17·3

Reported Song Frequencies for Some Birds

Species	Vibrations per Second		
	Mean	Highest Note	Lowest Note
Eastern Wood Pewee	4,125	4,375	3,650
Black-capped Chickadee	3,300	3,700	3,025
American Robin	2,800	3,300	2,200
Hermit Thrush	3,000	4,375	1,475
Starling	3,475	8,225	1,100
Chat	2,600	4,400	1,275
Eastern Meadowlark	4,400	6,025	3,150
Western Meadowlark	2,500	3,475	1,475
Cardinal	2,800	4,375	2,200
Song Sparrow	4,700	7,700	1,900

Source: Albert R. Brand, "Vibration frequencies of Passerine Bird Song," *Auk*, 55(1938):266–267.

Music of Bird Song. Not only are there differences in the ability of different people to hear different pitches, but also in individual understanding of what is actually heard. Although most bird songs are generally considered pleasing, some are definitely musical in the human interpretation of the word. That is, some bird songs contain musical tones arranged in the form of brief melodious phrases. Not all listeners are able to distinguish between songs that are musical in a general way and those that are musical in the way that our own music is musical.

Bird songs are esthetic expressions the medium of which is sound. They are rhythmic in the way that poetry is rhythmic. Many bird songs contain musical tones that can be recognized with more or less ease by persons with musical hearing. Yet even musicians may need to listen intently over a considerable period of time before it becomes clear to them what tones are sung and in what order. Some songs are intricate, high-pitched, and rapid to the extent that the aid of the physicist may be necessary to decipher them. The ornithologist, the physicist, the recorder of bird voices, and the musicologist need to work hand in hand for a complete understanding of the more difficult songs. Each type of research is important.

Describing Bird Songs. A number of different systems have been devised to help people to recognize birds by their songs. No one system has been devised that is satisfactory for all songs or for all people. Songs are often described by means of syllables, catch-phrases, or sentences that suggest the sounds. The Eastern Towhee does seem to sing "See Tow Hee-e-e" or "Drink Your Tea-e-e" and the White-throated Sparrow seems to sing "Old Sam Peabody, Peabody, Peabody." Diagrams are often found helpful, demonstrating the typical patterns of rhythm, pitch, syllabification, volume, and so forth. Verbal descriptions likewise shed light upon the nature of songs. Combination methods have been devised by some writers.

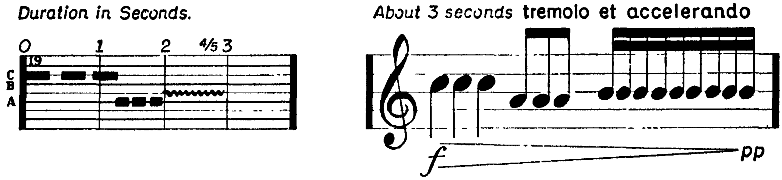


Fig. 17·10. *The "Saunder's diagrams" use horizontal lines to indicate notes and their length; vertical spacing indicates pitch; heaviness of the lines shows loudness. The Field Sparrow song diagrammed on the left has been transferred to the musical scale on the right.*

There are so many different aspects of bird song that perhaps the best suggestion is that we go into the field and study them at first hand. Musically trained listeners may wish to use musical notations to describe the melodious aspects of bird song where these are present; those who are not musically inclined, however, had best use one of the other methods of description. The "Saunder's diagrams" have proved useful for many listeners to bird songs. In many cases, the songs so diagrammed may be readily transferred to the musical scale (Fig. 17·10).

The song of the Yellow-billed Cuckoo provides an example of the sort of song that is unsuitable for description by means of musical notation. This song depends for its esthetic effect upon voice quality, range, rhythm, syllabification, changes in velocity and volume, and in pitch. This is poetry rather than melody, "wordless poetry," or "toneless music."

To be truly musical, as our own music is musical, the songs of birds must contain musical tones. The essentials of music are said to be *rhythm*, *melody*, and *harmony*. Yet music need not contain harmony as we use it today. It need be only melody. Melody is very old, but harmony—that is, harmonious tones that are sounded simultaneously—has been used by man for his enjoyment only in recent centuries. Yet the best folksong has always been founded on an unconscious feeling for the principles of harmony.

Music is natural rather than invented or discovered by man. Music is composed of musical tones of a given key successively (and sometimes simultaneously) sounded in a rhythmical way. It must be pleasing, according to the definitions. Both the selection of tones within the octave and their arrangement have physical and mathematical bases. Birds as well as human beings are intuitively aware of music and some in both groups are able to use it for their own purposes. A more limited use of musical tones is found elsewhere among living creatures, for example, in the utterances of frogs and toads.

Although most songs are musical in a general sense or in a poetic sense, not all contain melody. One of the simplest songs that is musical in the melodic sense is the whistled "phoebe" or "feebee" song of the Black-capped Chickadee (Score 1*a*, 1*b*, Fig. 17·11). It contains two tones of the musical scale in musical relationship. The song of Score 1*a* contains a *melodic interval* called a *minor third*; Score 1*b* contains a *minor second* interval. The song of the Eastern Meadowlark in Score 2 is a brief melodious *phrase, idea,* or *subject.* A song of the Western Meadowlark, shown in Score 3, contains melodic intervals and also a *harmonic interval,* uncommon in bird song.

Few birds are known to sing harmonic intervals or *chords,* although the study by physicists of recordings may provide us with additional species that do so. (The term "*harmonic interval*" is a musical term, not to be confused with the term "*harmonics*" used by physicists.) One of the birds whose songs contain chords is the Wood Thrush. This singer of the woodland can sound as many as four tones simultaneously. The listener may gain a fleeting impression of arpeggios and chords from this bird's singing, but the song is often so rapid that it is difficult to separate one tone from another without intensive study.

Melodic intervals are far more often heard in the songs of birds than are *harmonic intervals.* The Black-capped Chickadee sings two tones in the musical relationship of a minor third, a major second, or a minor second interval, sung in descending order. The Carolina Chickadee sings three or four tones with the above-named intervals and also several others occurring in the course of its wider repertoire. The Black-capped Chickadee's two-tone songs are so short that it does not seem important to know their musical key or tonality. The four-tone songs of the Carolina Chickadee are long enough to suggest definite tonalities. Both major and minor intervals are found throughout the Carolina Chickadee's songs. A very long list could be made

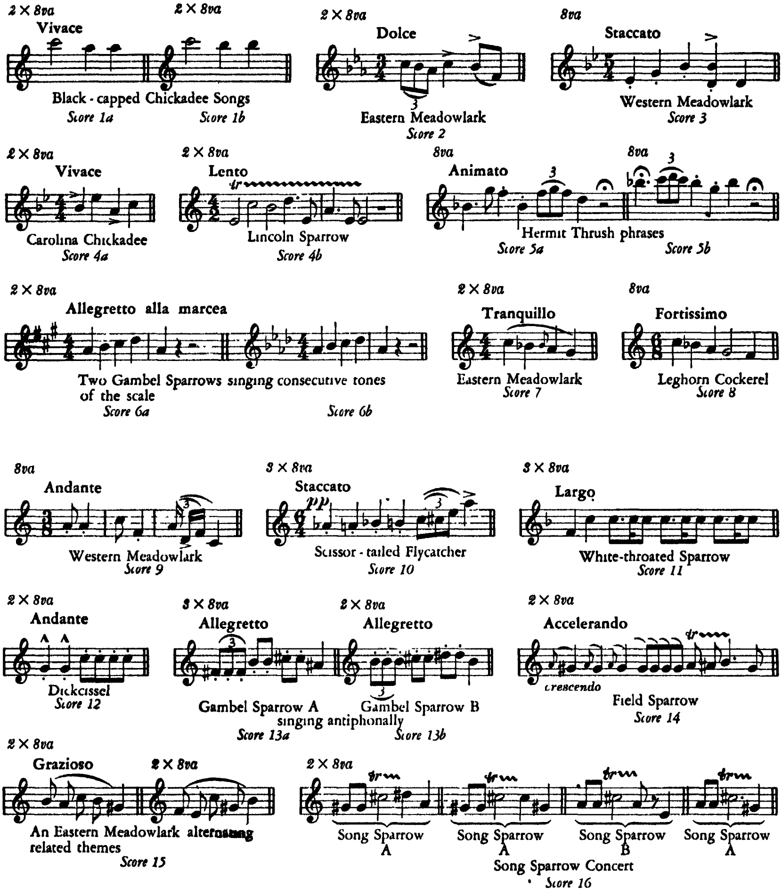


Fig. 17·11. *Musical scores of birds.* (*Taken from life by Anne Hinshaw Wing.*)

of birds that include melodic intervals in their singing; such a list would include Finches, Thrushes, Meadowlarks, Wrens, Warblers, and many other birds.

Melody results when a succession of tones of a given tonality are rhythmically sounded to express a musical idea. The effect upon the human listener varies with the melody and with the manner in which it is sung. A melodious phrase creates a certain impression in the mind of the hearer. If the tones belong to a major diatonic scale, a positive or joyous feeling is engendered in the mind of the human listener; but if the tones belong to a minor diatonic scale, a negative or mournful feeling is engendered, for reasons unknown. Perhaps birds may also feel the same influences. Pentatonic melodies vary in effect somewhat according to the order of succession of the longer and shorter intervals.

Musical Scales. The octave is an interval that is easily understood and recognized. Within the octave, five tones, each musically related to the starting tone, have been recognized in human music from ancient times. Chinese, Scottish, North American Indian, and other music, including folksong of many nations, all are built upon *pentatonic* scales. More highly civilized peoples have added two intermediate tones, forming the seven-toned *diatonic* scales. Some other groups use additional tones (termed *microtones*), the resultant music sounding strange to European and American ears, but fundamentally the music of all groups appears based on the natural scales of five or seven tones.

The use of tones and intervals varies with birds according to the species, although it is far from satisfactory to state once and for all that a given species sings only in such and such a manner, for birds are often surprising. The Prairie Warbler sings chromatic intervals and perhaps also microtones. The Hermit Thrush and Western Meadowlark seem to sing in the five-toned scale, with some exceptions. The Purple Finch, Gambel's Sparrow, White-crowned Sparrow, Song Sparrow and Eastern Meadowlark commonly use the diatonic scales, major and minor, seven tones within the octave.

It is difficult to state that the birds always use what we call *pure* or *just intonation*, but it is safe to state that they do not ordinarily use the *tempered* scale of *fixed intonation* by which our pianos are tuned. If a bird's tones and intervals are far wrong, probably the songs are classifiable as *atonal*, or poetic song. If basically true, a note that seems too high or too low may be classed as a microtone if it seems intentional, or as slightly different in intonation from human music. Perhaps birds, like humans, occasionally sing off-pitch. Southern Meadowlarks tend to sing off-pitch at the very beginning and very end of the breeding season, their melodies becoming clear in the height of the season. Song Sparrows sing less and less clearly as the summer wanes, until their voices are hoarse, their songs short, and musical tones seem almost absent. White-throated Sparrows sometimes *flat* toward the end of their songs, the tendency being perhaps more noticeable in late summer. Western Meadowlarks exhibit the rhythm and general pattern of the species song in early spring, but tone relationships are then unrecognizable. Little variation in intonation is heard from the Black-capped Chickadees at the various seasons in which they sing. Birds with melodious songs with true tone relationships are reported from many different parts of the world. Examples are shown of the singing of two North American species, the Carolina Chickadee and the Lincoln Sparrow, in Score 4*a* and 4*b* (Fig. 17·11).

The rhythmic arrangement of bird songs varies from simple to complicated. Ornithologists usually time in seconds the length of the song and of its parts. Musicians consider the main and subordinate accents in music, giving the musical "time" of the song. Gambel Sparrow's music often has four principal beats, suggesting *four-four* or *common time*. The music of the Southern Meadowlark varies, but some songs can be assigned *waltz time*, or *three-four* time. Some bird song tends to increase or to decrease in velocity, and one can use verbal indications to describe the change. Usually considerable musical training is needed in order to make the type of description used by musicians. However, musical indications are widely understood, and most bird songs are suited to this type of description. As in musical notations of North American Indian music, a change of rhythm may be indicated where it occurs.

Responsive Singing. Birds of the same species often respond musically to one another, continuing or varying a musical idea. Birds of different species sometimes influence one another's singing, so that the same tones and intervals may be heard in the singing of more than one species in an area. An Eastern Towhee at Ann Arbor, Michigan, not only used some of the tones of a nearby Song Sparrow but also changed its own type of song to correspond to some extent with the Song Sparrow's song. Birds are often aware of the whistled tones of human beings, and sometimes show this awareness by responding in kind or by stopping their song. Black-capped Chickadees and Mockingbirds show this type of awareness.

Rhythmic duets are sometimes sung by two birds of a single species. Male and female Chachalacas combine their songs into a unified whole. Black-capped and Carolina Chickadees sometimes do this also. The antiphonal singing of two birds may be linked in precise rhythm or it may not. In any event, the relationship of the melodies in the alternation of melodious songs is evident.

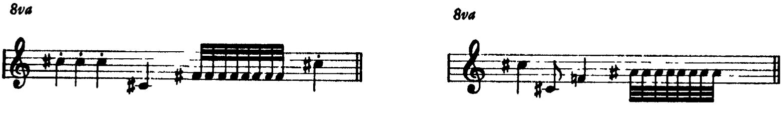
Bird songs are usually short and unfinished by human standards. The Eastern Wood Pewee sometimes achieves a sense of finality by so ordering the succession and selection of phrases that a cadence is effected. The bird, however, fails to stop there, and the process takes place over and over. This is a phenomenon of the twilight singing of this species. Two Gambel Sparrows may alternate songs rhythmically, the one song being a variation upon or a continuation of the other, some degree of finality being achieved in some instances. Again, however, the birds do this over and over. A Song Sparrow tends to repeat a song a number of times, then vary it so that, whether or not the bird is aware of the fact, some sense of musical cadence is achieved. Eastern Meadowlarks may alternate related themes. Hermit Thrushes have a limited number of themes but repeat them over and over in so many different orders of succession that finality appears, becomes lost, and reappears, no real cadence having been reached. Birds appear able to vary their tone successions so as to satisfy some feeling for musical continuity and cadence, following intuitively the natural laws of music used in a higher degree by human musicians.

Melodic variation is widespread among birds, some species appearing to extemporize. The Eastern Meadowlark and the Song Sparrow have many musical ideas and seem capable of inventing others at will. One song seems to suggest the next, and a succession of songs sung at a single sitting often seems musically related. An interruption or a period of silence may be followed by musical phrases in another mood. Each species sings in its own characteristic way most of the time, so that regardless of the melody of the moment, the accustomed listener can recognize the species by the song. Sometimes some characteristic of voice quality is the key to recognition when there is doubt, or it may be a characteristic rhythm. Occasionally the same melody occurs in different species. On the other hand, individual Song Sparrows in nearby territories at Brady's Bend, Pennsylvania, sang certain individual songs in so characteristic a manner that they could be distinguished by their melodies. In addition, these territory defenders sang other and less characteristic songs.

In spite of melodic variation in the songs of a species, the kind of music sung is typical of the species as a whole and may even be typical of related species. Among species of Chickadees there may be found a relationship in melody, some songs of the Carolina being similar to some songs of the Mountain Chickadee, whereas others suggest those of the Black-capped Chickadee. Similar musical relationships may be found among the members of the Thrush family. Both tone successions and song patterns may be to some extent inherited, the ability to vary the song differing according to the species.

Birds often seem to take their cues from other singers about them. As mentioned previously, they frequently employ the same musical tones in some parts of their songs. Sometimes they may even alter their typical manner of singing in imitation of the song of another species. People who depend entirely upon *quality* for distinguishing bird song could never notice this. Sometimes several birds of different species may be heard singing in the same musical mode or key. A

Song Sparrow near Ann Arbor, Michigan, for example, sang several repetitions of a song related to that of the Red-eyed Towhee (Fig. 17·12). The principal difference serving to distinguish it musically from the singing of the Towhee consisted of the three staccato notes on one pitch that began the song. No sooner had the Song Sparrow ceased singing this song than the Towhee, rather hesitantly at first, began to sing. The Towhee began on C-sharp, as had the Song Sparrow, but with one note only, then descended to the C-sharp an octave lower, as had the Song Sparrow, then rose to F-natural instead of F-sharp, as if uncertain of what had been sung, then followed with



Song Sparrow Red-eyed Towhee

Fig. 17·12. *A Song Sparrow sings a song similar to that of a Red-eyed Towhee. Then the Towhee starts to sing its own song, although it had been silent before. (Taken from life by Anne Hinshaw Wing.)*

A-sharp, forgetting, one might suppose, that the Song Sparrow had sung C-sharp, as the Towhee might well have done. Earlier in the season, a Towhee in the same area sang in seeming imitation of a Song Sparrow, the two songs interfering, and the Towhee going out of its way to change the form of its song to harmonize with the song that the Song Sparrow sang at the moment. Many other birds may be heard from time to time imitating songs of other birds of different species or blending their songs with them, especially in the matter of pitch.

To review the foregoing pages, many bird songs suggest atonal syllables rather than melodies; some bird songs are commonly melodious only in part; and some birds usually sing melodiously throughout the length of their songs. There is much yet to be known concerning the musical behavior of birds. Much of the most remarkable music comes from some of the members of the Finch family (Fringillidae), the family of the Meadowlarks (Icteridae), and the Thrush family (Turdidae). These and other fine singers combine musical tones into brief melodious phrases comparable to the melodious phrases of similar length sung or played by human musicians. Although the bird music considered here is of North American origin, other writers have described as musical the bird song of other continents.

SUGGESTED READING

Cheney, Simeon Pease, *Wood Notes Wild: Notations of Bird Music.* Boston: Lee & Shepard, 1891.

Craig, Wallace, *The Twilight Song of the Wood Pewee* Myiochanes virens *Linnaeus: A Study of Bird Music*, New York State Museum Bulletin No. 334, 1943.

Ingraham, Sydney E., "Instinctive Music," *Auk*, 55(1938):614–628.

Mathews, F. Schuyler, *Field Book of Wild Birds and Their Music.* New York: G. P. Putnam Sons, 1921.

Nicholson, E. M., and Ludwig Koch, *Songs of Wild Birds.* London: H. F. & G. Witherby, Ltd., 1936.

Oldys, H. W., "Parallel Growth of Bird and Human Music," *Harpers Magazine*, 105(1902):474–478.

Rüppel, W., "Physiologie und Akustik der Vogelstimme," *Journal fur Ornithologie*, 81(1933):433–542.

Saunders, Aretas A., *Bird Song.* New York State Museum, Handbook No. 7, 1929.

Saunders, Aretas A., *A Guide to Bird Songs.* Garden City, N. Y.: Doubleday & Co., Inc., 1951.

Witchell, Charles A., *The Evolution of Bird-Song.* London: Adam & Charles Black, 1896.

18

Courtship and Nesting Habits

In the cold light and the figurative glare of biology, a bird may be said to live but for one purpose: reproduction of its kind that the thread of the species may remain unbroken. In reality, to accomplish this seemingly brief task takes much of a bird's effort. Because only a part of the year is suitable breeding time in most areas except for a few tropical ones, in a very real sense a bird survives during the nonbreeding season in order to function as a potential parent of the breeding season. Many other animals do likewise, but some forms of life can suspend operations during the unfavorable season, so to speak, by such means as encysting or calling "time out" as in aestivation or hibernation.

The reproduction habits of higher animals in general follow complex patterns and involve complicated behavior. These all seem to be functional. Because so many people are interested in birds, their breeding habits have been studied more than have those of any other class. The courtship behavior of birds includes remarkable performances. They have been shown repeatedly to embrace "formalized" rituals and ceremonies.

COURTSHIP BEHAVIOR

Function of Courtship. In the simplest analysis, courtship serves chiefly as the combination or magic "sesame" unlocking the door of reproduction. Only the right turns of the figurative biological dials permit the pairing of birds. In so doing, courtship provides much of the reproductive isolation in the bird world. "Psychological isolation" during the breeding season may operate through differences in plumage, voice, or habits (Skutch, 1951). The intricate courtship pattern of one species thus brings response and pairing with individuals of that species only. Without some channeling of the reproductive interests of the many species, each to its own kind, biological chaos would surely result.

Because birds cannot communicate and receive identification and sexual signals by scent (a rather accurate indicator of the reproductive and sometimes physiological state of a mammal), the complicated courtship behavior of birds may be a more involved way of accomplishing the same thing. By means of visual and vocal signals, the sexes may (a) clearly and recognizably indicate the desire for pairing, (b) stimulate each other, or (c) reach a satisfactory state of accord. A male already in the prime of the seasonal sexual cycle might very well pass beyond the efficient stage for carrying on his share of the reproductive burden if mated to a delayed female. To illustrate this, one might imagine a resident male Robin in Oklahoma pairing off in the spring or wasting his early reproductive possibilities on a female Robin migrating to the Yukon and not ready to breed for many weeks to come. Clearly, it is an advantage to the species for its members to signal to each other their state in the breeding cycle, automatically or upon demand.

Recognition of Sex. The sex of birds having marked sexual dichromatism (or other sexual dimorphism) often may be recognized by appearance (see Chapter 8). The presence of the "moustache" of the Flicker (page 131 and Fig. 7·17) identifies its wearer as a male to males and females alike (Noble, 1936). Probably birds recognize the opposite sex instinctively. A young Mallard female, newly adult and previously inexperienced with the male, having been reared by the mother alone, recognizes the green-headed male as such. Most birds seem able to recognize the cues or signals of sex, whether vocal, visual, or behavioral, with little if any trial and error period. Yet it must be recognized that learned habits (*imprinting*) may influence many things in bird life. Most if not all birds reared under alien circumstances if free to do so would return to the ways of their kind, though the road might prove a rocky one. The young Cowbird in the summer or fall deserts the foster species to consort with its kind; a female Cowbird is able to recognize the male, though reared alone in a foster home. The same may be said of birds reared by hand; yet one should interpret with caution happenings in the lives of zoo birds and others exposed to man's confinement.

Species having the sexes alike, and many others, evidently distinguish sex largely by action, either alone or in combination with sounds.

A male and female Song Sparrow meeting for the first time in the spring and often after long acquaintance react in the manner customary to the sex. A male bristles up to a stranger, which, if it is another male, reacts aggressively in kind or flees; but if it is a female, the stranger will probably crouch submissively or in an inviting manner, often with a peculiar call, or flee (Nice, 1939). But the English Robin has to learn the hard way, it seems, for the female may be the more aggressive. Sex recognition appears by no means to be instantaneous; the female searching for a mate persists in returning to the territory, whereas other females move off (Lack, 1946). The Yellow-eyed Penguin, however, always knows the sex of another bird (juvenile or adult) on sight, though the sexes look alike. The observer himself learned to distinguish females by their "sheepish look," and presumably the Penguins themselves could do as well (Richdale, 1951).

The whole subject is a complex one. Birds may interpret (hence recognize) various signals to mean various things at various times, not necessarily of a sex-recognition nature, and methods of sex recognition are still largely unknown to us. In any event, birds may clearly get to know each other as individuals (page 383 and Fig. 19·5). Bobwhites can detect strangers in the covey. Common Terns will recognize their mates in the air; mated Pintails identify each other at 300 yards from the nest and English Robins at 30 yards. The Smooth-billed Ani distinguishes individuals. Song Sparrows know each other, Black-headed Gulls know their associates, and the Crimson-crowned Bishop Birds know their neighbors (Armstrong, 1947, 1950).

Mating Habits. Animals follow several patterns of mating habits, which have been termed *polyandry*, *polygamy*, *promiscuity*, and *monogamy*. Monogamy is probably the most usual rule of mating in the bird world. At the minimum, the duration of the mating bond in monogamous pairings may be short, almost momentary and for insemination only; for all practical purposes, this is really nonpairing. In some species, the pairs may remain mated for some time, usually until incubation begins. In more constant ones, a pair may remain mated through one brood, remating often with each other for subsequent broods. In many common Passerine birds, the pairs remain mated through the season, sometimes raising several broods during the period of the mating bond. Some birds, (e.g., Geese, Swans, and larger predators) may form a mating bond for life. Monogamy may be seen to result in pairing off in unions of varying length.

Polyandry occurs rarely among birds. It may indicate a probable surplus of males, though reliable figures are difficult to find. The Button-quails (*Turnix*) and Painted Snipe (*Rostratula*) practice polyandry (Mayr, 1939). It occurs at times among species in which the female takes the more aggressive role in courtship behavior, as among the Phalaropes. A *pseudopolyandry* in which several bachelor males attach themselves to mated pairs has been reported in Central American Bush Tits. Attachment of a bachelor Bob-white to a mated pair has been reported.

Polygamy is the form of polygyny having one male mated with two or more females. For it to function successfully as a species characteristic, as distinguished from sporadic or irregular occurrence, the males apparently must outnumber the females. This has been noted in several species, either by means of *differential mortality* or *deferred maturity* in the male. Species practicing polygamy usually have the family duties—nest building, incubating, caring for the young—done by the female alone. Grouse tend to be polygamous, as are the Turkey and various Pheasants. The Red-winged Blackbird among Passerine birds may practice polygamy. In the case of the Red-winged Blackbird and Ring-necked Pheasant, the several females establish subterritories within the territory of the male, which subterritories they hold against each other (page 226).

Sporadic polygamy has been reported in many birds, some of them otherwise rather rigidly monogamous, others less rigidly so. Among monogamous birds known to have had polygamous examples are such birds as the House Wren, American Robin, American Marsh Harrier, Song Sparrow, and White-crowned Sparrow. Sporadic polygamy among the Passerine birds probably occurs with greatest frequency among the Weaver Finches.

Whether or not true promiscuity occurs among birds as a rule of mating habits rather than as aberrant behavior has not been determined clearly. It has been reported for the Ruff. It is presumed to occur among Grouse whose males gather at mating grounds to which the females resort for insemination. The Cowbird among Passerine birds is reported to be promiscuous, but its habits only give that appearance because the Cowbird lacks the ordinary nesting behavior (Laskey, 1950).

Courtship Patterns. Three general patterns of courtship can be recognized, though there are numerous variations and overlappings. The patterns may be listed as *communal, competitive* or *nonterritorial,* and *territorial.* It may well be that further knowledge of the individual courtship patterns of the many thousands of species unstudied will revise considerably our knowledge of these matters, just as it no doubt will with many other phases of bird life.

Prairie Chickens, Sage Grouse, Sharp-tailed Grouse, and Black Grouse illustrate the workings of *communal courtship,* the first of the three patterns thus distinguished. The males gather at favored courtship grounds (called variously by such terms as *leks*, *arenas*, *booming grounds*, and *dancing grounds*) to which the females come.

A large number of birds pair off while still in flocks, while on the winter grounds, when in migration, or when in the breeding range, such as among many Waterfowl and other water birds. Because this appears in public, so to speak, and thereby invites competition and interference from others, it may be termed *competitive* or *nonterritorial* for convenience. The majority of common birds, however, take up a territory before pairing off. *Territorial* courtship is therefore rather private, and the territory dominates its occurrence. Territorial courtship implies initiative in the female as measured by her searching for territory or for a male fixed in his territory.

Mate Selection. We have little actual knowledge of what determines or signals the actual mate selection as distinguished from the courtship performance itself. Much has been written about selection as a form of evolution, but little of selection as a form of choice in bird life. In many territorial birds, selection or choice of a mate seems to be something of a haphazard or chance affair. Birds tend to return to their previous territories, the places familiar to them, so that chance is subject to this trait. A female searching for a mate may exercise some choice of selection, but it may be that she pairs off with whatever male she is with at the crucial moment of her sexual state. It may be that much of the choice may actually be selection by mutual tolerance or perhaps even by default. A male or female using the same area may mate by the simple process of accepting the situation without any serious "screening" other than for being of the same species and in the appropriate sexual condition.

But when two or more birds compete for one of the opposite sex, the matter is clearly not so simple as this would indicate. A common Tern indicates acceptance of a mate by exchange of a fish or other offering. A female Mallard indicates her selection when flying by allowing one male of several contenders to fly alongside her and perhaps by touching him with her bill. In the water, the male bobs his head and an accepting female bobs back. But just how the majority of birds signal acceptance of each other as mates is little known. It may be that the acceptance is really signaled by mutual use of the behavior patterns that mated pairs use with each other—which might indicate that if the birds do use them, they are mated, if not, they are not mated.

Courtship Performances. In a sense, courtship is a series of display performances, often with calls and songs, though sometimes per-

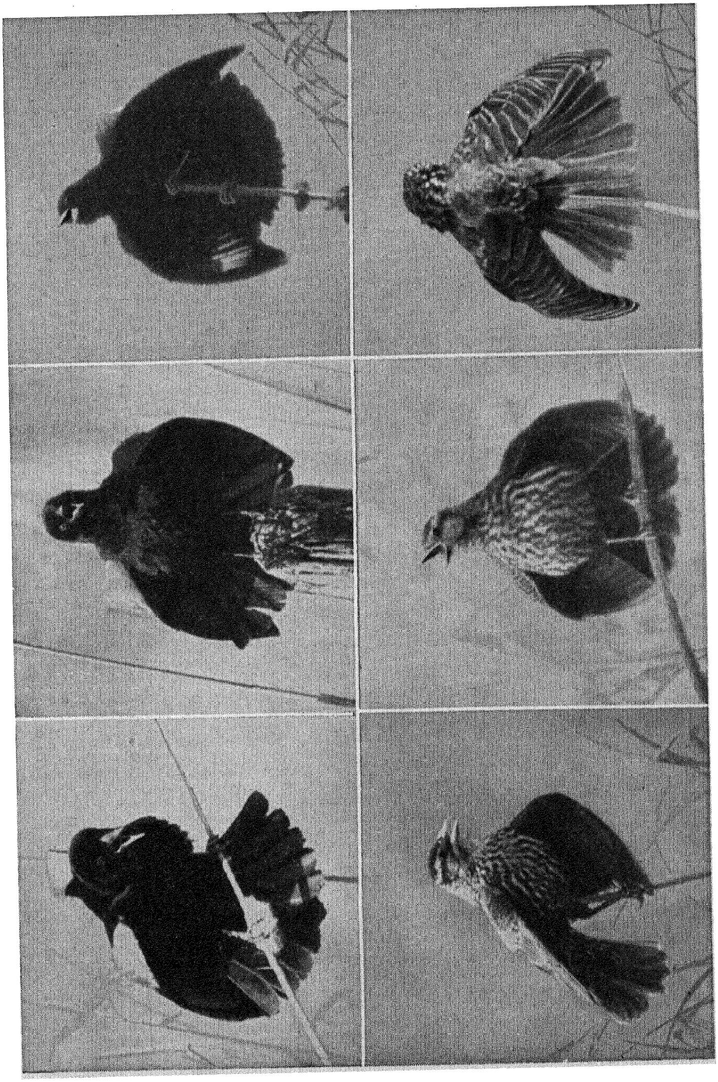


Fig. 18·1. *The use of the same postures in display performances by the male and female show clearly in these photographs of male (upper) and female (lower) Red-winged Blackbirds. (Photograph by Robert Nero.)*

formed only by posturing and displaying of the plumage (Chapter 7). The number and variety of display performances seem limited only by the number of bird species. Sometimes those of the male and female are very much alike (Fig. 18·1). Because each species has several to many meaningful poses, perhaps destined to *release a response* (Tinbergen, 1948), the total number in the bird world is almost astronomical. Numbers of them have already been described (e.g., Armstrong, 1947). Many birds, for example, put on "courtship flights" involving both male and female, the former usually the pursuer, the latter the pursued. Often special songs or calls are part of the flight. Some involve display of color patches, like the white throat and white wing patches especially accentuated by the Nighthawk. The flight gait itself may involve differences peculiar to nuptial flight.

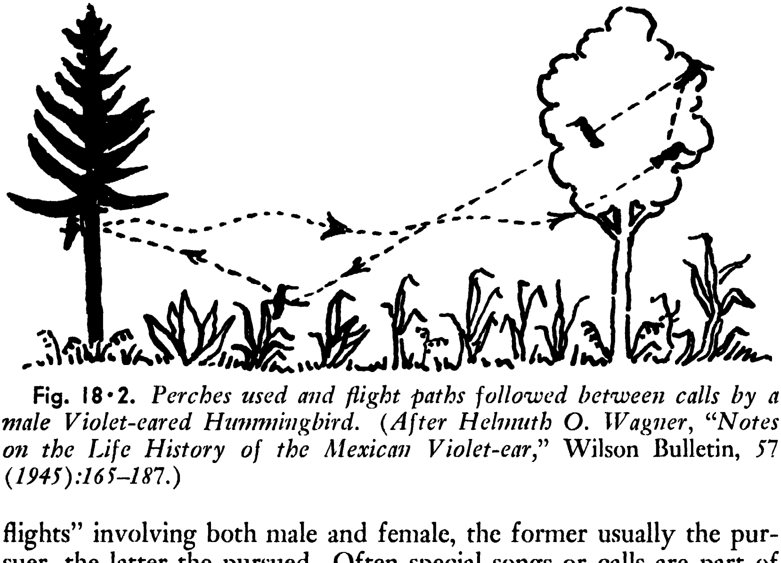


Fig. 18·2. *Perches used and flight paths followed between calls by a male Violet-eared Hummingbird. (After Helmuth O. Wagner, "Notes on the Life History of the Mexican Violet-ear,"* Wilson Bulletin, 57 *(1945):165–187.)*

Courtship flights in some birds may be by the male alone. The flight song of the Vermilion Flycatcher (see Fig. 17·8) is in a sense a courtship flight. (It should be recognized, however, that distinction between courtship and territorial behavior has not been clearly established.) A variation in which the bird calls from a perch but changes perches between calls (averaging 2 minutes and 40 seconds apart) occurs in the Violet-eared Hummingbird (Fig. 18·2). Many birds of the open prairie or marsh have courtship flights involving both male and female (which if mated may more properly be considered as *nuptial flights*) or the male alone. That of the American Marsh Harrier is particularly well known. Even some birds of the forest, like the

Red-breasted Nuthatch, Woodcock, and Ovenbird have courtship flights.

The courtship postures and displays of some game birds have been studied in considerable detail. Fig. 18·3 shows several poses of the Ring-necked Pheasant, male and female. But no less elaborate in many cases are the performances of other birds, some of which involve complex dances associated with equally complex actions. There is a conspicuous correlation between the movements of a displaying bird and its special charms of form or coloration. The Lady Amherst Pheasant erects the neck-ruff on the side turned toward the female. A Ruby-crowned Kinglet (see Fig. 7·18) erects his crown, the Umbrella Bird exhibits his bright-red air pouches, and the Snow Bunting displays his back pattern to the female (Fig. 18·4).

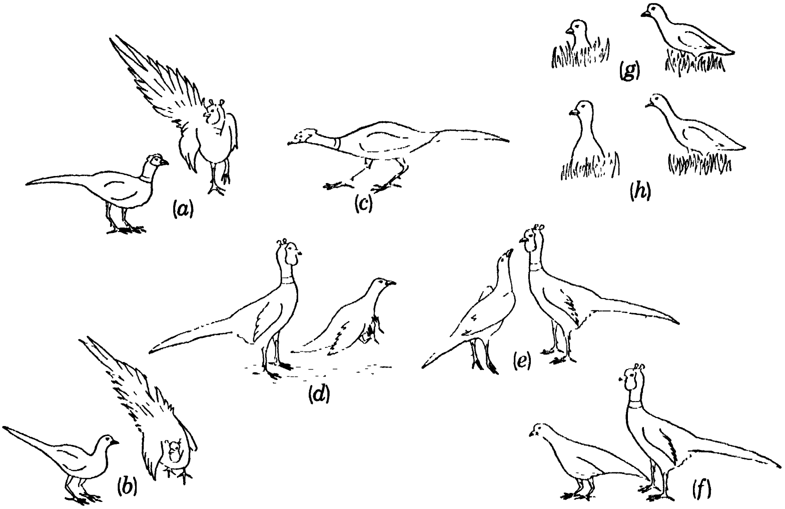


Fig. 18·3. *Postures of male or female Ring-necked Pheasants. (a) Intimidation display of dominant male to submissive male, (b) courtship display of male to female, (c) pose of nonterritorial male while trespassing in the territory of another, (d) "flirting hop" posturing of a female, (e) stretch posture of female to male, (f) half-squat posture of female, (g) posture of hen without chicks, neck not stretched, (h) posture of hen with chicks, neck stretched. (After Richard D. Taber, "Observations on the Breeding Behavior of the Ring-necked Pheasant,"* Condor, *51(1949):163.)*

One of the most striking of performances is the distinctive upside-down display of several Birds-of-paradise, all famed and resplendent exhibitionists. Male Bowerbirds, near relatives of the Birds-of-para-

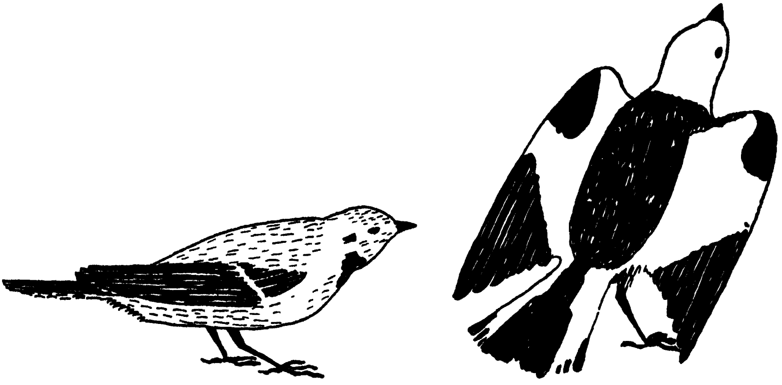


Fig. 18•4. *Back display of the Snow Bunting. The male displays his variegated black and white pattern, and in so doing, walks slowly away from the female, his back toward her. (After N. Tinbergen, "Social Releasers and the Experimental Method Required for Their Study,"* Wilson Bulletin, *60(1948):6–51.)*

dise (also of New Guinea and nearby islands and Australia), have the unique habit of building tiny ceremonial houses (bowers) and walks furnished with display objects (usually blue in the Satin Bowerbird's bower, which species also has intensely blue eyes) (Marshall, 1950). The whole process of the male's display before the bower appears to be substitution of an inanimate object for the primary sexual attraction itself and may serve in maintaining sexual stimulation despite establishment of territory early and at a time highly disadvantageous for reproduction. To add to the several remarkable features of the performance, some males make a "paint" or charcoal of fruit pulp mixed with oral secretions and apply it to the inside of the bower by means of a soft, fiber swab. This has been suggested as having some remote connection with courtship feeding, perhaps as a substitute offering to a substitute object.

Incubation and Courtship Feeding. Males of many species feed the incubating female, perhaps the best-known example being that found among the Hornbills. The female of the Hornbills incubates while the male feeds her; she has been imprisoned by the male who closed the hole except for a port through which he passes food.

Courtship feeding, as distinguished from incubation feeding, has been reported among birds in more than forty families of sixteen orders. Among common birds, courtship feeding seems unreported in Loons, Grebes, Petrels, Grouse, Auks, Woodpeckers, Thrashers, Starlings, Vireos, and Weaver-finches. In others, courtship feeding varies from a regular trait to a rare event (Lack, 1940).

In the act, the female usually adopts an attitude and uses calls almost identical with those of a young bird begging for food. The male may put the food into her mouth. Some birds regurgitate food for the female; the male Herring Gull deposits it on the ground, and the male Pigeon feeds from his crop. The Common Tern is especially known for using a fish in courtship feeding. Even the common barnyard rooster calls the hens to food. In the Button-quails, the female is reported to feed the male. Substitutes for food may be offered. A Tern may present a stick instead of a fish. The Adélie Penguin offers snow, though this seems to be done during incubation and may be related to incubation feeding. The Gannets merely touch bills together, which may be the minimum act in the performance. "Billing and cooing" by some birds may be a substitute for courtship feeding, just as touching the bill in the Gannets may be the minimum of the substitute.

Because courtship feeding seems not primarily concerned with food as nutrition (which incubation feeding seems usually to be), it may be a vestigial act now part of display and courtship. It has been suggested that the infantile parent-child relationship in this way may be symbolized in adulthood. Its primary function may be to maintain the mating bond, for it is found mainly among those species in which both sexes care for the young. Of this, however, there are marked exceptions. In some species, courtship feeding seems a necessary prelude or signal for copulation.

Copulation. In its immediate purpose, courtship functions to establish a harmony between the sexes to accomplish insemination of the female at the proper time in the reproductive sequence. The dominance of the male over the female (*sex dominance*) also plays its

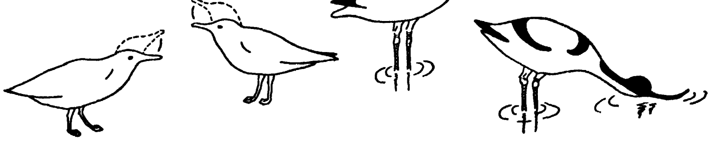


Fig. 18 • 5. *Signals or stimuli may precede copulation as in the "begging movements" of the Herring Gull (left) or the "preening movements" of the Avocets (right). (After N. Tinbergen, "Social Releasers and the Experimental Method Required for Their Study,* Wilson Bulletin, *60(1948): 6–51.)*

part in providing a submissive receiver. But only when birds have been stimulated sufficiently and at the proper time will copulation take place. The sight of birds copulating may induce imitation or suggestion in others, but it may also elicit attack on the copulating pair.

In some species, copulation occurs upon invitation of the female or in response to a vocal signal. It may occur with little preliminary ceremony, the female merely squatting. But in most birds, the male seems to initiate the preliminaries or they may be largely mutual. Usually this involves such actions as body contact, billing and cooing, nodding and bowing, flight pursuit, or even preening (Fig. 18·5). The preliminaries may be violent buffeting or seemingly violent attacks by the male upon the female; but violent though this may be, it appears to be a regular part of the ritual in some species.

The amount of semen produced in the Domestic Rooster varies from 0.05 cc. to 1.00 cc. per completed copulation. The sperm count averages nearly a billion for each discharge (Parker *et al.*, 1942); the number of spermatozoa ranges from none to ten million per cubic millimeter and averages about three million, a count substantially greater than that in domestic mammals. The spermatozoon measures about 90 microns in length, three-quarters of which is tail, a part lost soon after reaching the oviduct (see Fig. 6·1).

Generally the period during which copulation occurs lasts but a short time, and copulation usually ceases when the first egg is laid. In some species, copulation may occur a month or more before egg laying, more than 2 months previously in the Gentoo Penguin (Richdale, 1951). Yet copulation in autumn and even on the winter grounds 3,000 miles from the breeding range has been reported for the European Roller (Armstrong, 1947). Fertilized eggs seem to be laid not earlier than the second day after copulation. Experimentally, the percentage of fertile eggs from domestic hens declines rapidly in a week or so after the last copulation. But Sage Grouse hens lay no eggs for two or three weeks after copulation, which seems to occur but once annually (Scott, 1942).

BREEDING ACTIVITIES

Breeding Seasons. In but few species of the equatorial regions have ornithologists found much evidence for truly nonseasonal breeding (Baker, in DeBeer, 1938). In higher latitudes, breeding is annual in the course of the seasons. As someone has said, it follows the sun. But in the Tropics and Subtropics, the breeding season has a complex character; yet seasonal events in nature are not entirely absent. In the wet Tropics, nevertheless, no regularly recurring period is available to which breeding season control may be related (Baker, in DeBeer, 1938), and ornithologists sometimes tend to postulate some rhythmic, internal control.

The egg season of eight species of Coots (Subfamily Fulicinae) with wide latitudinal distribution illustrates the tendency for some species to show two breeding seasons in the Tropics. Each season, in fact, is that of the respective Northern or Southern Hemisphere carried into the Tropics and even across the Equator (Fig. 18·6). The birds breed earliest in the middle latitudes and later toward the poles and Tropics, though data from the Southern Hemisphere are not sufficient to demonstrate this clearly. In some species, however, the egg season becomes progressively later from the tropical region poleward in both hemispheres, that in the Southern being half a year behind that of the Northern Hemisphere.

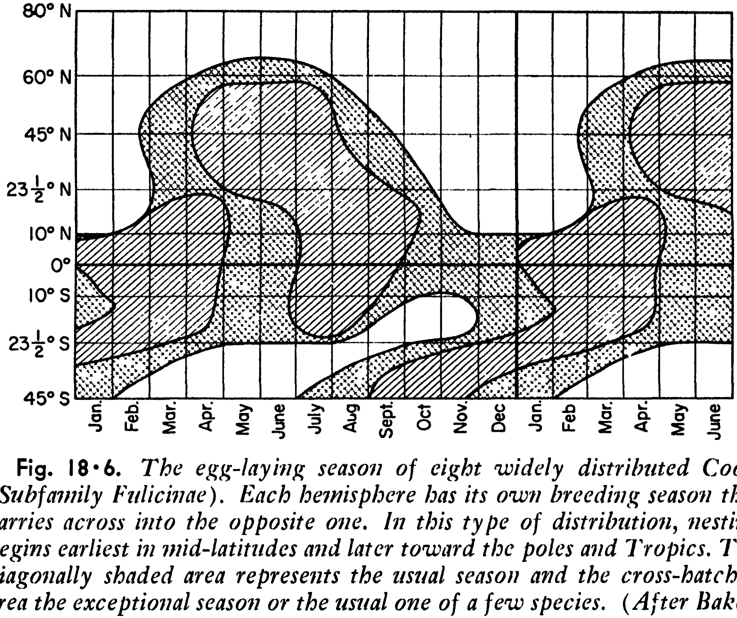


Fig. 18·6. *The egg-laying season of eight widely distributed Coots (Subfamily Fulicinae). Each hemisphere has its own breeding season that carries across into the opposite one. In this type of distribution, nesting begins earliest in mid-latitudes and later toward the poles and Tropics. The diagonally shaded area represents the usual season and the cross-hatched area the exceptional season or the usual one of a few species. (After Baker, by permission from* Evolution—Essays on Aspects of Evolutionary Biology, *ed. by G. R. DeBeer, p. 165. Copyright, 1938, The Clarendon Press, London.)*

But some species seem insensitive to latitude and breed at about the same time throughout their ranges. The Secretary Bird, for example, breeds in July and August in the Sudan north of the Equator, as well as in tropical South Africa.

The Sooty Tern usually breeds in the appropriate spring or early summer season north or south of the Equator, with a tendency to breed earlier nearer to the Equator. Yet local controls may influence this, as may also the apparent source of the breeding birds. Birds ranging perhaps in the northern oceanic region may return south to breed at times different from that of nearby birds from the Southern Hemisphere. That might explain differences in breeding time, such as of Terns nesting on some Hawaiian islands in both June and November (Richardson and Fisher, 1950).

A most interesting breeding-season rhythm, possibly the most unusual yet reported by ornithologists, occurs among the Sooty Terns of Ascension Island, 8° South Latitude in mid-Atlantic. The Tern, known locally as Wideawake, breeds in large colonies called "fairs," hence "Wideawake Fair." The members of the fairs disperse over the tropical South Atlantic but return to Ascension Island to breed (page 292) at intervals averaging about 9.7 months (Chapin, 1954). A time chart shows that the pattern measures exactly ten lunar months, which may be only a coincidence. No known environmental periodicity accounts for the special timing, and a physiological relaxation period has been suggested. In the Seychelles Islands of the western Indian Ocean, the Sooty Tern breeds in July and August, their arrival and breeding time apparently being governed by the monsoon (Moreau, 1950).

The nesting dates of the Horned Owl in North America from Florida northward show well a latitudinal progression (F. M. Baumgartner, 1938). How it may operate southward is not known. Nesting in southern Florida begins in late November, in New England in early February, and in Labrador in late March. This gives a northward shift of 85 to 90 miles of latitude for each week of spring. The breeding season starts later by 3 to 4 days for each degree of latitude and 100–125 meters of altitude, which accords with the Hopkins bioclimatic law (Johnston, 1954).

Length of the Breeding Season. It may be considered as axiomatic that for each species the breeding season is long enough to raise the minimum number of young maintaining the population. But it should not be said that birds necessarily breed everywhere as rapidly or as slowly as they can. Bird life in the middle and higher latitudes of the Northern Hemisphere has a pronounced seasonal rhythm readily seen by even the most casual observer. Birds, for all practical purposes, can be said to breed beyond the Tropics in the "spring" of the year, but one must recognize a lack of precision in

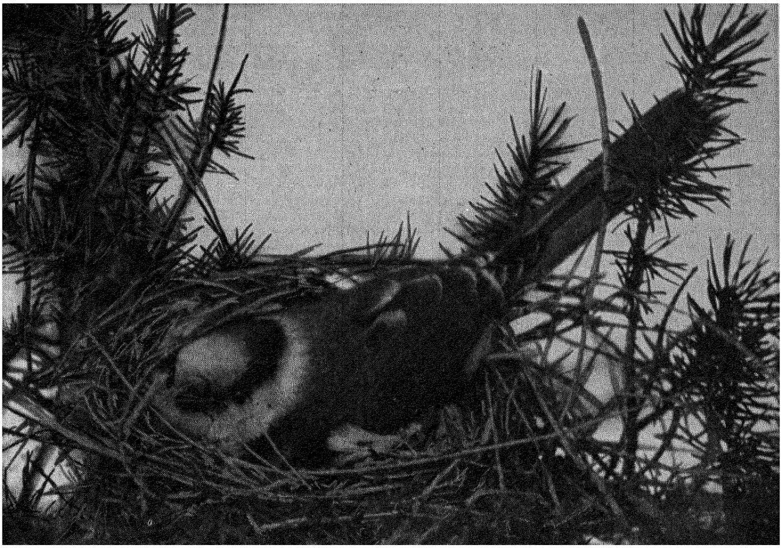


Fig. 18·7. *Canada Jay on nest at 10° F. below zero, Prince Albert, Saskatchewan, April 1. (Photograph by Fred G. Bard.)*

such a generality. A few birds, for example, begin nesting in the early winter or even late fall along the tropical side of the middle latitudes. Bald Eagles in Florida may start repairs to their eyries in the last week of September or in early October and may begin to lay eggs by the first week of November (Broley, 1947). Individual Eagles are usually consistent in nesting (i.e., in being either early or late), some nesting several months after the early ones. Individuals and colonies of Brown Pelicans have on occasion nested earlier each succeeding year to push nesting forward from February and March to October.

Among early nesting birds are the Horned Owl and Horned Lark, which may nest in northern United States and southern Canada so early that snow may yet cover the nest. The Canada Jay regularly nests early, often long before snow has left the northern woods, when the temperature may be below zero (Fig. 18·8). By its insulation, the thickly constructed nest no doubt aids greatly in preserving the needed high incubation temperature.

Some birds may be consistent late nesters. The American Goldfinch, for example, regularly waits until practically midsummer before nesting, long after most other birds have started and many have finished. The Gray-crowned Rosy Finch of the snow line in the Rockies nests late also, as does the Evening Grosbeak.

Many birds start early and nest more or less continuously throughout a long season from early spring until late fall, often bringing off several broods. But others nest but once or twice during a relatively fixed interval. Among the former are the Mourning Dove, House Sparrow, and Cardinal that nest in some parts of the United States from February or March until September or October. But many species, especially though not always in the northern regions, nest for a short season only.

Seasonal Variations. Anyone who has recorded the finding of nests will soon be aware of differences in the time of first nests or the peak of nesting from year to year (page 213). An observer in New York state found that Black-capped Chickadees laid the first egg about May 5 in 1941, some two weeks earlier than in 1940, when the first laying was about May 18.

It has been demonstrated that the phases of the nesting season may be more or less telescoped in the North as compared to farther south. The White-crowned Sparrow at the Canadian border uses less than two-thirds of the time taken by those of central California for the active part of the reproductive cycle (Blanchard, 1941). A comparison of Prothonotary Warblers (page 364) nesting in Tennessee and Michigan (about 400 miles farther north), for example, shows that the latter birds nest later, use less time in preparatory activities, have larger eggs, lay larger sets, and only occasionally attempt second broods. The nesting season varied from 69 to 73 days in Michigan and from 101 to 128 days in Tennessee (Walkinshaw, 1941).

Conditions Influencing Breeding. That the environment influences the activities of birds hardly seems necessary to mention. The ways by which it may do so seem almost limitless, so many and so diverse are they. In general, the environmental influences fall conveniently into such common classes as light, climate (or weather), and vegetation.

In the long run, suitable conditions for rearing of young, such as food and cover, may be the underlying determinant to which birds have become adjusted. Biologists have long known that light, either as a total amount or a daily increase (see Chapters 6 and 16), will bring birds into breeding condition. But the actual breeding itself may be retarded or suppressed when territorial or social conditions are unsuitable. An example of this may be found in the reservoir of birds unable to find territory for themselves and thereby not breeding, yet they may do so if territories become available (page 257). Cool temperatures have repeatedly been shown to delay nesting just as warm ones may accelerate it. But cool temperatures within the usual variations of the habitat seem unable to stop breeding, even though delaying it.

Birds of tropical regions may be attuned to wet and dry seasons irrespective of calendar months. Presumably they are governed by events leading up to the season (in which they breed) or perhaps the birds have much shortened the preliminaries that begin after the coming of rains. There are examples of birds that in dry tropical regions breed before the rains, though most seem to await the start of the rainy season (Baker, in DeBeer, 1938). The famed Finches of the genus *Geospiza* in the Galapagos Islands breed when the rains begin; it is said that the sound of falling raindrops stimulates captive birds to sing (Lack, 1950). In wet tropical regions with well-marked differences in rainfall, birds tend to breed toward the end of the wet season. But in wet tropical regions with less well-marked differences, breeding tends to take place, for the most part, in the drier part of the year.

Many birds of the Arctic fail to breed because of failure to find safe nest sites, inability to find good cover, or because of shortage of food (Marshall, 1952).

Influence of Social Stimulation. The influence of imitation or suggestion should not go unnoticed. In close quarters, as on the nesting grounds of colonial birds, the action of one bird or pair may be taken up by others. Early pairing activities of one or two birds in a flock may set off this behavior in others. Nest building by a single pair of Terns seems sufficient stimulus to start a series of nest constructions by others, just as a sudden flight by one bird in some flocks may be the impetus to cause all to fly. But it should be expected that these reactions would be stimulating only to favorable subjects. When a population drops below a minimum level, the lack of social stimulation may be important in biological success (Darling, 1938).

NESTS AND NESTING

Selection of the Nest Site. Among birds that form no lasting mating bond and among polygamous ones, it is usual for the female alone to select the nest site. In the common birds of the field, forest, and garden, the male selects the neighborhood, usually alone (see Chapter 12). But it hardly seems reasonable to suppose that a male selecting a territory would be unaware of potential nest sites. Preferences in sites are clearly instinctive, and it seems logical to suppose that a male carries such instincts in his inherited make-up, just as does the female. Their expression, however, may be inhibited in the male or stimulated in the female, for she generally takes the initiative.

Among birds having very special nesting-site requirements, the male may actually select the site, often well in advance of finding a mate. The shortage of holes and the competition for them among hole-nesting birds, for example, make successful breeding dependent upon the male having found one when the finding was good—namely, early in the season. A male House Wren arrives ahead of the female and promptly seizes upon a nest box in the garden as the center of his territorial attentions. The male House Sparrow takes over some cranny as his own and chirps his territorial claims. As soon as a female appears upon the scene, he pops in and out to signal his possession and, it may be supposed, the suitability of the site; no doubt it serves also as an enticing gesture for a responsive female.

Within the territory of the male, the female looks for suitable nest sites, often attended by and on occasion helped by the chirping and singing male. The female (and sometimes both) tries out forks, tangles, and other likely sites by squatting in them—as though for the feel of the site. But on occasion, the female apparently rejects all sites within the male's territory and chooses one beyond. When this happens, the male must add the new area to his realm, often by fighting it out with another in possession. Even among those species in which the male selects the actual nest site, the female may turn it down and build in a new place. Some males build a partial nest at the site or place there some nesting material, which may be added to by the female, thrown out altogether in favor of a fresh start, or rejected for some other site.

Nest Material. Birds do many things that seem marvelous to us, and construction of a nest surely is one of them. A newly adult female, at her first nest-building job—an inexperienced bride, so to speak—builds a complicated nest in every way the typical nest of her progenitors, whether she lived in one like it or grew up in an artificial environment. (Among some species, succeeding nests have been found superior to earlier ones, which indicates improvement with maturity and experience.) Yet the ability of the bird to weave, entirely by instinct, challenges the imagination (Fig. 18·8).

Birds generally use the handiest material, but selection characterizes the species and to some extent the larger taxonomic groups. Birds of a genus and family, for example, tend to build rather similar nests. But there are many exceptions and variations, especially among birds of wide adaptive radiation, like the Icteridae. Common birds use mosses, lichens, grasses, fibers, stems, and small twigs. Substitution of man-made or man-associated materials may occur (see Table 10·2). The American Goldfinch that uses plant fluff will build a nest of cotton or sheep's wool. Wrens have used wire clippings in place of the usual sticks. American Robins often use string, yarn, or twine. Chipping Sparrows had no horsehair available before the coming of white man in America, at least not since the Pleistocene. Horsehair seems to be but a substitute for fine plant fibers.

Special nesting material, however, may be the vogue for some species. The American Robin builds a nest reinforced with mud and fiber. A Barn Swallow builds a mud nest on the beams of a barn as a substitute for a protecting cliff wall, broken tree, or hanging ledge.

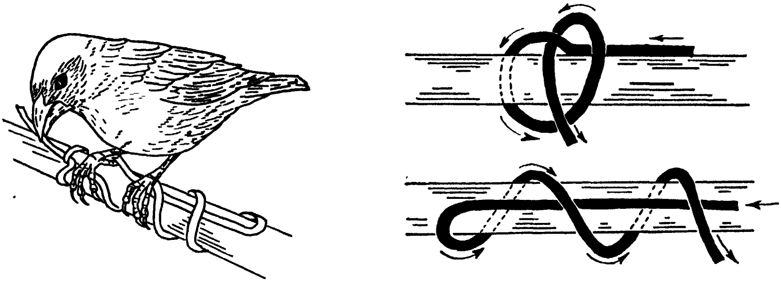


Fig. 18·8. *Weaving by the Red-billed Weaver-finch.* Left. *The bill serves as the shuttle, the feet holding the weaving strip to the limb.* Lower right. *Simplest and most commonly used stitch.* Upper right. *A stitch used in conjunction with the lower one. Arrows indicate direction of weaving.* (*After Herbert Friedmann, "The Weaving of the Red-billed Weaver Bird in Captivity,"* Zoologica, *2(1922):355–372.*)

The Cliff Swallow, however, goes a step further; it builds a retort of mud stuck to a cliff. Yet it will use the eaves of a barn or the concrete of a bridge. The "glue" that holds the mud together comes from the oral secretions, as it does also in the Swifts (page 61).

Few birds go far for nest material, a few score yards at most for the average dooryard bird and seldom more than a few dozen rods for any bird except possibly those needing special material. Eagles may bring articles long distances, but usually only when the nest is finished.

A great many individual pieces make up the nest of a Magpie or Bald Eagle. The former may be as big as a wash tub, the latter a dozen feet across. A nest of the Alta Mira Oriole from Tamaulipas, Mexico, measured 6 by 8 inches in diameter and 20 long; it contained by count 3,387 separate pieces of grass and plant fiber, many from 36 to 50 inches long, the total weighing 131.1 grams, air dry. A Rose-throated Becard nest from the same state measured 10 by 11 by 19 inches in size and contained 1,844 separate pieces of leaves, twigs, grasses, and fibers, several from 18 to 41 inches long, the total weighing 342.7 grams, air dry. A Purple Finch nest from the Adirondacks of New York measured 6 by 5 by 5 inches and contained 753 separate pieces, largely grass, several from 10 to 15 inches long, the total weighing 53.2 grams, air dry.* The Becard and Finch measure less than 6½ inches in length, the Oriole but 9. One must surely credit such birds with expenditures of relatively prodigious amounts of energy. If one were to hazard a guess, perhaps 400 to 800 pieces would be average for the number of items used in building a Passerine nest.

Nest Construction. It has been said that in general if the male differs strikingly from the female, especially if he is brightly colored, or if he is an ardent and adept musician, he takes little part in the nest building. But when males and females are alike, they may work together on the job, or the male may bring nest material but the female does the actual fitting of it into the nest structure. Among common birds, the male helps some either by carrying nesting materials as in the Cardinal, or by helping in the actual construction as in the Crow. All possible variations seem to be found. The male of some, perhaps most, Weaver-finches, for example, usually does all the building; but among the Orioles, the female builds the nest. Among hole-nesters that excavate their own cavities, both sexes generally work together. The male and female Woodpeckers and Kingfishers also work together on the hole as well as the nest chamber. Both sexes of Cliff, Barn, and Bank Swallows participate in nest building.

Once started, nest construction may be very rapid, though like other things in nature, variations occur. Usually birds start nest building shortly after forming the mating bond; it appears to be delayed in some, like the American Goldfinch. Sometimes Woodpeckers may excavate a cavity the fall before and use it for winter roosting quarters and often for nesting later on. First or early season nests usually take longer than later ones. Ten Prothonotary Warbler nests constructed in May required 7, 6, 11, 8, 2, 3, 2, 4, 6, and 4 days respectively to build; nine constructed in June required 6, 1, 1, 1, 4, 1, 1, 1, and 1 days (Walkinshaw, 1938). Birds of the short seasons of higher latitudes take less time than birds of related species or of the same species farther toward the Equator (page 360). The Alta Mira Oriole may use 3 to 4 weeks in building a nest in Tamaulipas, but the Baltimore Oriole farther north builds in 10 to 12 days.

The Red-billed Weaver, when given a choice of color, showed preference in this order: red, orange, yellow, green, blue, violet, and black. The last three named, however, may not have been used in significant amounts (Friedmann, 1922).

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* Original data.

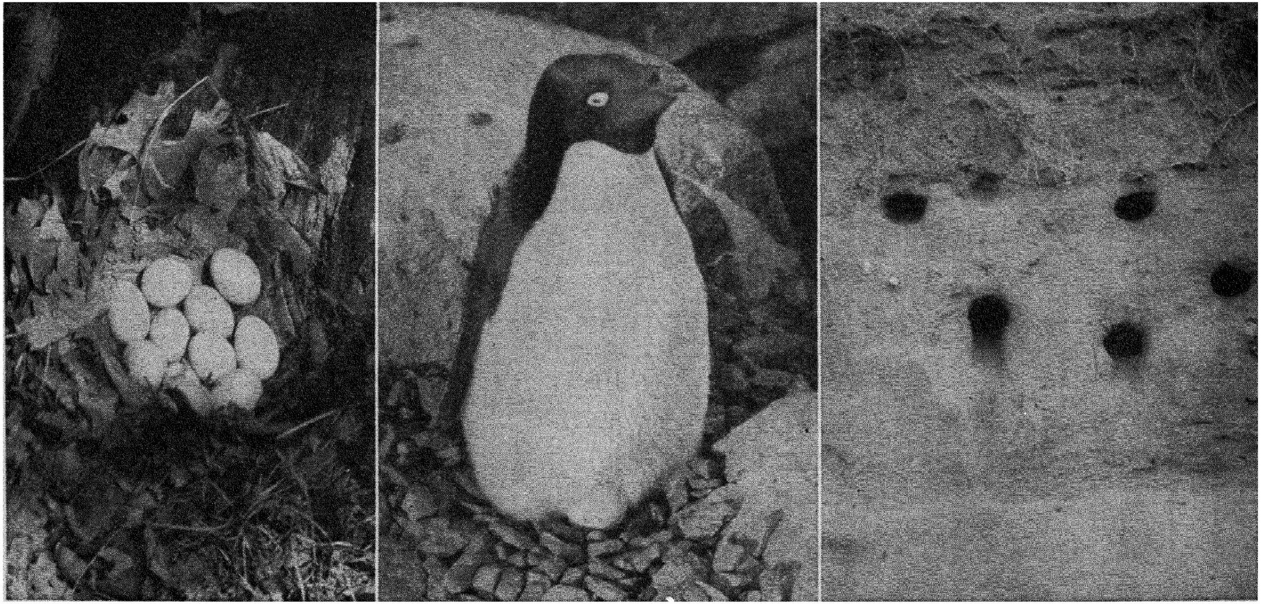
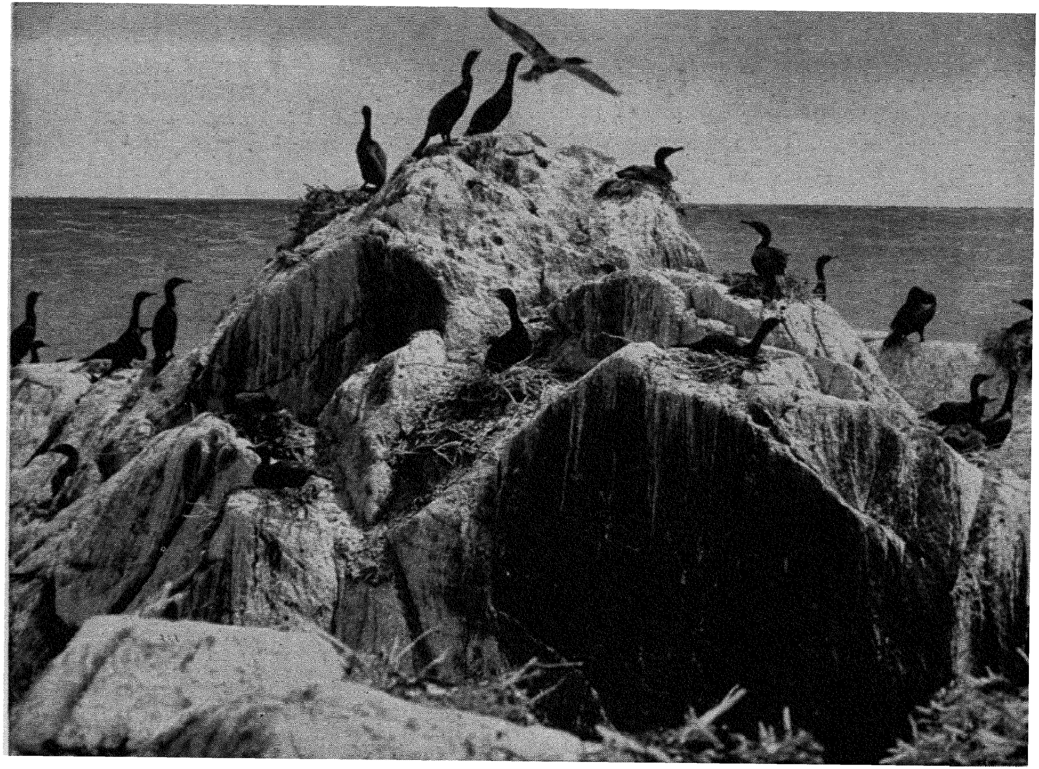


Fig. 18·9. *Some sites chosen for nesting.* Left. ***Ruffed Grouse nest on the forest floor*** *(photograph by Wisconsin Conservation Department).* Center. *Adélie Penguin nesting on shore among the rocks (photograph by U. S. National Archives).* Right. *Bank Swallows burrow into banks for nesting (photograph by Leonard W. Wing).*



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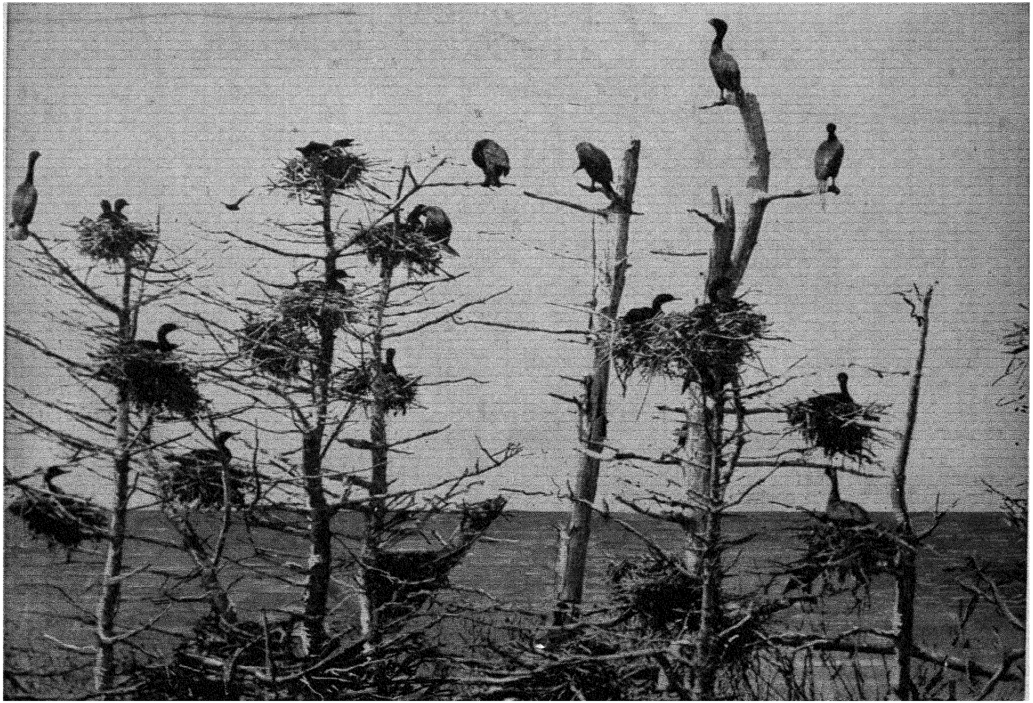

Fig. 18·10. *Cormorants may nest on rocks if protected from ground enemies, as on an island (top), or in trees elsewhere (bottom), particularly if suitable ground sites may not be present. The nest is a bulky affair on the ground or in a tree.* (*Photographs by Alfred O. Gross.*)

Nest Location. Each species has an instinctive pattern of choice for a nest site (Fig. 18·9). The Cardinal seeks vines, bushes, thickets, and similar places for nesting in all parts of the range. A Mourning Dove chooses a tree limb or a clump of twigs that provides a suitable platform. It may nest on the ground. Most New World Warblers prefer forks among the branches, but the Prothonotary chooses a cavity, the Kirtland the ground, and the Yellow a bush. Cormorants nest on rocks of islands and headlands, and some colonies may take to the trees (Fig. 18·10). Herons and Egrets nest in trees and sometimes in bushes of off-shore islands along the Gulf of Mexico.

Throughout many groups of birds runs the habit of nesting in tree cavities (but this does not indicate relationship). Ducks, Hawks, Parrots, Owls, Flycatchers, Swallows, New World Warblers, Chickadees, Nuthatches, Wrens, Thrushes, and Weaver-finches have species that nest in holes. Few of these are able to make holes of their own, which in a sense seems to be the mark of "true" hole-nesters like the Woodpeckers.

The height above the ground varies, but each species tends to follow a pattern. Some may be high nesters like the Red-eyed Vireo, others consistently low like the Catbird, and many others intermediate in choice. A Mockingbird nest may be as low as 5 feet or as high as 30 feet from the ground. The Mourning Dove usually puts its nest 10 to 30 feet above the ground, but some have been found lower, even on the ground. The Canada Goose normally nests on the ground, but it may use old nests high in trees. Geese have been found nesting on cliffs not far from others nesting on river bars along the Snake River in Washington.

The amount of concealment of the nest varies also, even in the same species and among closely related ones. No satisfactory rules between concealment of nest and conspicuousness of the parents seem in order, though possibly some relationship does exist. It has been said that where both sexes are equally conspicuously colored, nests tend to be little concealed. An evolutionary adjustment between the chief enemies, competitors, and elements on the one hand and the breeding birds on the other may contribute a large measure of influence upon nest location.

Origin and Evolution of Nesting. Little has been written of the possible evolutionary origin of nesting—with the exception of song and possible exception of bird migration, the most conspicuously distinctive breeding characteristic of all animal groups. Because some form of nesting occurs among many other and less highly developed vertebrates (reptiles, amphibians, fishes) as well as in invertebrates (wasps, ants, spiders), it may well be that nesting antedates the origin of the bird itself. One proposal suggests that the use of more elaborate structures by birds originated in the advantages over their cold-blooded neighbors that insulating or protecting material dragged to a nest gave to birds. From this simple beginning developed more elaborate structures. But the origin of nests in great antiquity leaves us with little to go on save what we can interpret from our knowledge of living birds.

THE EGGS AND THEIR INCUBATION

Laying Hours. Birds as a general rule lay their eggs before mid-morning (Skutch, 1952). Nocturnal birds appear to reverse the laying cycle. Some birds perhaps follow a somewhat modified schedule, but the secretive nature of egg laying makes precise information rather difficult to obtain. The deposition of the egg may require from a few seconds to several minutes at the nest. The most rapid laying seems to be that by the Old World Cuckoos and American Cowbird, parasitic species and hence ones for which it might be unprofitable to linger long in the nest of another (page 108).

The most common birds lay their eggs about a day apart. Some species, however, seem to be consistently different in the laying interval. The Mourning Dove is said to lay its two eggs about 36 hours apart,* an African Swift (*Micropus caffer*) at 2-day intervals, and the Red-beaked Hornbill at intervals of 5 to 7 days (Moreau and Moreau, 1940).

Number of Eggs. The number of eggs (often called "clutch-size") varies widely among species and seems related to the kind of life. Birds with precocial young lay more eggs than comparable birds with altricial young. Evidently the nest and associated parental care provide greater security for raising young than the ground or water. Within general limits, it is clear, the number of eggs reflects the life hazards. Thus migratory species tend to lay more eggs than non-migratory ones. But as pointed out in the discussion of breeding potential (page 247), the number of attempts in the reproductive lifetime of the bird probably indicates best the effort needed by the species—which is to match the mortality rate in the population.

Among altricial birds, certain definite tendencies may be detected. Birds with longer nestling periods lay larger sets than those with shorter ones. The number of eggs laid by Passerine birds varies with the species, being greatest in the hole-nesters and progressively fewer in those with roofed nests, nests in niches, and open nests, which trend also parallels the shortened nestling periods (Lack, 1947, 1948).

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* *Wilson Bulletin,* 55:198.

Birds of the Tropics lay significantly fewer eggs than do their relatives in higher latitudes, a general rule believed to apply within genera and families as well as within the species. Fringillids of middle Europe, for example, average 5.0 eggs to 2.6 for tropical ones, Shrikes 5.5 *vs.* 2.5, and Rails 8.6 *vs.* 3.8. The increase with latitude parallels a tendency for increase from west to east and occurs among Passerines, Herons, Hawks, Gallinules, Terns, gallinaceous birds, and a few others. This tendency appears absent in Loons, Petrels, Gannets, and Doves (Lack, 1947, 1948). The average clutch-size seems to bear some relationship to the ability of the parents to provide food in the region and in the season. The fact that species having long nestling periods lay many eggs (hence have many young to feed) has suggested the idea that with the same amount of food or food-gathering ability available, a large family can be raised slowly or a small one rapidly.

The number of eggs laid in a clutch declines in the course of the season, though it may rise temporarily in the early part of the nesting period of species with long laying seasons. Successive clutches of the Wild Turkey have been noted to decline from eighteen to twelve and finally to ten eggs. Sets of the Field and Chipping Sparrows (total 104) averaged 3.39 and 3.66 eggs respectively but declined seasonally, as shown in Table 18·1. The number in the Great Tit averaged 10.8 before the third week of April and 9.0 after, while that of the Blue Tit averaged 11.1 before and 8.4 after (Gibb, 1950). The American Goldfinch averaged 5.0 eggs per set during the first half of July, 4.8 the first half of August, and 3.4 the first half of September.

Table 18·1
Average Number of Eggs Reported

Species	May	June	July	August
Field Sparrow	3.77	3.69	3.14	3.0
Chipping Sparrow	3.91	3.69	3.28	3.0

Source: Lawrence H. Walkinshaw, "Nesting of the Field Sparrow and Survival of the Young," *Bird-Banding,* 10(1939):107–114, 149–157.

Renesting and Multiple Nesting. Among most birds, renesting will take place if the nest is destroyed. But such renesting is subject to the time of break-up of the nest and the stage of the breeding season. If late, renesting usually does not occur. The estimate has been ventured that not more than 10 per cent of the actual attempts at nesting produce young, and less than 20 per cent of the completed ones may endure until the young leave of their own accord (Allen, 1930). Some birds lay eggs within 5 days of nest destruction, though the interval varies in different species and at different stages in their nesting.

Multiple nesting differs from *renesting* in that it involves nesting again in the same season after the successful production of one or more broods. Renesting, on the other hand, is the successive attempt of the bird to bring off a first brood. The Bob-white very rarely if ever raises two broods in a season. Yet a pair whose nests are broken up may continue all summer to try to bring off its biological quota of one brood. Because a female Bob-white nesting for the first time may do so later in the season than older ones, nests of young females may be confused with renesting attempts of older birds.

Incubation Periods. The length of incubation has been discussed in Chapter 6, largely from the embryological standpoint (but see Table 6·1). Many inherent difficulties face the field student studying incubation periods. For one thing, attentiveness to incubation is not consistent among species and individuals alike. Some seem to take up incubation duties rather lackadaisically before settling down to regular habits. Others faithfully cover the eggs from the start. Among species in which only one sex incubates, some time off the nest for feeding is necessary. But among those in which the male and female share, the eggs may be covered nearly all the time. The incubation period for practical purposes should be measured as the interval between laying of the last egg in completed sets and hatching of the last nestling (Skutch, 1945). But in the Great Tit, "apparent incubation" begins any time from 3 days before until 3 days after completion of the set (Gibb, 1950).

In some other birds, such as the Road-runner and Hornbills, incubation begins with the laying of the first egg, and the young hatch several days apart. The significance of this trait has not been determined with any satisfaction. In one or two species, only one of a pair of differentially hatched young survives. But in most, death of the smaller bird probably results from its position of disadvantage in a nest of larger ones. But most species of middle and higher latitudes begin incubation with the laying of the last egg, or within a day or so before or after.

Careful study at the nest indicates that much coming and going may take place among Passerines, not at all like the unmoving vigil of a setting hen in the barnyard. The diurnal bird alternates periods of attentiveness and inattentiveness throughout the day. Data reported for several species show averages in minutes as follows: Allen Hummingbird on 18.2, off 4.3; Yellow-headed Blackbird on 9.1, off 5.4; House Wren on 14.3, off 6.0; Black-headed Grosbeak on 29.2, off

10.3 (seconds). In all but the Black-headed Grosbeak, incubation is by the female only; in the Grosbeak, the male incubated 36.7 per cent of the time, the female 62.8 per cent (Weston, 1947). Other reported percentages of time during which the eggs were incubated are: Song Thrush 58.7, Yellow-headed Blackbird 63.9, Hedge Sparrow 66.4, European Nuthatch 73.0, Song Sparrow 76.5, Chiffchaff 77.5, Ovenbird 82.5, and Marsh Tit 84.0 (Fautin, 1941). But among large and robust birds (perhaps also those less highly tensed), protracted periods of incubation may be expected. A Buller Mollymauk, for example, incubated continuously for 24 days, though a constancy of 6 to 11 days at a sitting seems to be average for the female (Richdale, 1951).

The length of the incubation period obviously varies among species. Among the various factors related to it may be listed the taxonomic position of the species, the size of the egg, and ecological factors (such as dangers to which the nest is exposed) (Skutch, 1945).

The incubation urge lasts long enough to include the time necessary for the normal incubation period and a margin of safety. Ordinarily, the urge seems to run out a few days after the expected time of hatching. But some seemingly extraordinary constancy to sterile eggs has been reported. Evidently a bird could be expected to carry on beyond the expected hatching date for as long as a third to a half of the incubation period.

In any discussion of incubation by birds, whether by male, male and female, or female alone, one cannot escape mention of unusual cases of two groups of birds that depend upon nature to do it for them (excluding social parasites). The Brush Turkeys of the Australian region bury their eggs in a pile of vegetable matter scratched together; the heat produced by decomposition of the plant material supplies warmth. They have been found to use sun-warmed sand and even volcanic-warmed earth, where they dig a hole 1 to 3 feet across and to a similar depth in which a dozen or so eggs are buried. The birds may tend the "incubator" up to hatching time. The Black-backed Courser of North Africa is said to have taken on the habit of burying its eggs in warm sand (Allen, 1925).

By a special anatomical development, many incubating birds develop a "brood patch." The feathers on the breast are shed several days before laying the first egg and the skin somewhat thickens to bring about more intimate contact between the eggs and the warm body. The feathers come in again at the fall molt (Barley, 1952).

Nest and Egg Mortality. It has already been said that a surprisingly large number of the attempts at nesting fail to produce flying young. But this does not mean that a pair may not raise young because the first attempt failed, for most common birds try and try again. There seems to be no such thing as a nest secure from all disasters. Even that of the great Bald Eagle may be lost by breaking of the tree holding it. A nest in a seemingly impenetrable thorn bush can be approached by a more competent animal than man. Yet nests vary widely in their degree of safeness, some being more so than others. The size of the nest in itself is a protection, as is also the size of the parents. The firmer the construction, the safer is the nest. Placement, concealment, and many additional things influence the safety of the nest. Even the size of the colony bears upon the matter in colonial species (see Chapter 14).

In general, nest destruction becomes less frequent toward the poles, toward the dry lands, and toward the higher elevations. The last is illustrated by the destruction of 85.7 per cent of the nests in the lowlands of Panama compared to 44.8 per cent in the Guatemalan highlands (Skutch, 1945). But the destruction of nests and eggs does not necessarily imply a net loss to the bird. An American Robin may start to build several nests within a matter of weeks before finally raising a brood of young. The percentage of nest destruction thus might appear appalling, but one nest built by the pair having succeeded, the "pair success" would be 100 per cent. In general, nest success of altricial birds averages about 43 per cent, that of hole-nesters about 66 per cent * (see also Chapter 6).

Many eggs fail to hatch for various reasons, chief among them being "infertility." Embryonic deaths occur principally at three critical periods, a happening said to be specific for birds. For the Domestic Chicken, these fall on the (a) third to fifth, (b) twelfth to fourteenth, and (c) eighteenth to twentieth days (Romanoff, 1949). A study of the Arctic Tern showed a variety of causes for nest and egg loss, none of which was a major factor in itself. Of the 144 eggs laid in 100 nests, 91 hatched and 15.9 per cent fledged young (Pettingill, 1939).

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* *Bird-Banding*, 23:55.

SUGGESTED READING

*ALLEN, ARTHUR A., *The Book of Bird Life.* New York: D. Van Nostrand Co., Inc., 1930.

*ALLEN, GLOVER N., *Birds and Their Attributes.* Francestown, N. H.: Marshall Jones Co., 1925.

*ARMSTRONG, EDWARD A., *Bird Display and Behavior.* London: Lindsay Drummond, Ltd., 1947.

*ARMSTRONG, EDWARD A., *Bird Life.* New York: Oxford University Press, 1950.

BEACH, FRANK, *Hormones and Behavior.* New York: Paul B. Hoeber, Inc., 1948.

BULLOUGH, W. S., *Vertebrate Sexual Cycles.* London: Methuen & Co., 1951.

*DARLING, F. F., *Bird Flocks and the Breeding Cycle.* Cambridge, England: Cambridge University Press, 1938.

HERRICK, FRANCIS HOBART, "Nests and Nest Building in Birds," *Journal of Animal Behavior,* 1(1911):159–192, 244–277, 335–373.

*HERRICK, FRANCIS HOBART, *Wild Birds at Home.* New York: Appleton-Century-Crofts, Inc., 1935.

KENDEIGH, S. CHARLES, *Parental Care and Its Evolution in Birds.* Illinois Biological Monographs, 22(1952):1–356.

*LACK, DAVID, *The Life of the Robin.* London, England: H. F. & G. Witherby, Ltd., 1943.

LACK, DAVID, "The Significance of Clutch Size," *Ibis,* 89(1947):302–352, 90(1948): 25–45.

*NICE, MARGARET MORSE, "Problems of Incubation Periods in North American Birds," *Condor,* 56(1954):173–197.

RICHDALE, L. E., *Sexual Behavior in Penguins.* Lawrence, Kan.: University of Kansas Press, 1951.

*SMITH, STUART, and ERIC HOSKING, *Birds Fighting.* London: Faber & Faber, Ltd., 1955.

TINBERGEN, N., *The Study of Instinct.* Oxford, England: Clarendon Press, 1951.

TINBERGEN, N., *Social Behavior in Animals.* London: Methuen & Co., Ltd., 1953.

19

Young Birds and Their Care

The fact that the male in some species lets the female build the nest without his help or incubate the eggs alone afterward may not deter him from helping with family duties once the eggs have hatched. Sight of the young stimulates the male to start feeding in such cases (Skutch, 1953). Only the female Prothonotary Warbler and Field Sparrow incubate the eggs, for example, but the males of both species care for the young (Walkinshaw, 1938, 1939). In some species, as in the American Goldfinch, the male feeds the female while she is incubating (though she may get food for herself also), and he may help during early brooding of the young, but he participates in their feeding later. Some males feed the female who feeds the young or who gives food brought by the male to the young. But among monogamous birds, the males usually help, though their mates may do the greater share of the work.

EARLY GROWTH AND DEVELOPMENT

Hatching and the Newly Hatched Young. The imprisoned young pips the egg by violent exertions of the neck muscles, which bring the "egg tooth" atop the end of the bill against the shell until a hole opens. The young often alternate periods of activity and rest, though some young have been reported to chip the egg all the way around in a few minutes of effort. Continued movements of the head and body extend the cut until the end of the egg has been nearly severed. A few kicks sometimes and the bird has hatched. The interval between the pipping of the egg and hatching, however, seems to vary from about an hour to several days, depending upon the species. Some reported intervals indicate the possible range of variability: Sooty Shearwater, 4 days; Woodcock, 36–48 hours; American Goldfinch, 15–30 hours; and Ovenbird, 15–20 hours.

Hatching generally takes place in the forenoon, though some may be expected to hatch at any hour of the day (Skutch, 1952). Just what regulates such a rhythm for the bird within the protection of the nest has not been established. Perhaps the combination of darkness and light, cooling night temperatures, and the nocturnal lowering of body temperature in the incubating bird provides the control.

The newly hatched bird weighs less than the newly laid egg from which it developed, usually by a quarter to a third. The loss in weight is attributed to the egg shell and membranes, to dehydration, and to gaseous exchange. Because the young bird may get fed rather promptly in altricial species, it is seldom known for certain that a recently hatched nestling has not been fed. Eight young Great Tits definitely known not to have received food averaged 1.30 grams, while the egg of the species averages 1.75 grams in weight. The daily loss in weight during incubation was reckoned at 0.02 grams (Gibb, 1950). The newly hatched Blue Tit averaged 0.8 and the eggs 1.1 grams. Sterile eggs change weight but little, as does the unincubated egg (0.001 grams daily in the Great Tit). The young of the Tits weighed 74 per cent of the egg weight; the newly hatched Domestic Chicken weighs about 58 per cent of the egg weight.

The discarded shell may be thrust out of the nest by some young birds or left behind by precocial ones. But in altricial birds the job of clearing out the shells usually falls on the parents. Many adult Passerine birds eat the remnants of shells, but others carry them to a little distance from the nest before dropping them. (This act sometimes leads to the impression that nests have been destroyed or that the birds have been robbing nests.)

The newly hatched young of some species—Woodpeckers, Cuckoos, Kingfishers—wear no feathers, being completely naked or with but a few hairlike feather structures. Young of other altricial birds have a few tufts of down (the usual thing for Passerine birds) or have the body practically entirely covered with down (as in Hawks, Goatsuckers, and Herons). Precocial young carry a coat of down, damp at hatching but soon dry and fluffy. The young of some sea birds, such as the Gulls and Terns, are rather semialtricial. The chicks stay in the nest for some weeks but are covered with down and have about as much walking ability as true precocial young. They may roam for a few feet about the nest, but this wandering sometimes proves fatal to the young when they enter a territory other than that of the parents. The young of the Brush Turkey show more than the usual precocity. It hatches with a good coat of feathers, even of flight feathers, which unsheath before the bird reaches the surface of its incubator (page 372). The newly emerged young bird is reported as being able to fly. No other newly hatched bird flies at so early an age.

Altricial young usually have the eyes closed for a number of days, a condition varying with the species. The slightest jar on the nest (and sometimes sounds) will shortly cause the newly hatched young to uncurl the neck, thrust the head upward, and open the mouth for food. After the eyes open, the young tend to crouch down into the nest under the same circumstances and to respond mostly to the parental visit, often as the result of the chirps of the adult. Later they may flee the nest when disturbed. The greater the hunger, the greater the agitation of nestlings, so that the parent tends to put food into the most active and most extended mouth. (For this reason, the young Cowbird nestling may gain in the competition for food at the expense of the smaller occupants of the nest, which are unlikely to present so extended a mouth.) A fed nestling may still open its mouth and receive food, but a temporarily satiated bird may not swallow it. The parent may remove food not promptly swallowed and give it to another open mouth.

Growth Rate. The growth rate of birds varies widely, depending in part upon length of nestling period and size of the bird. The young increases its rate of growth a few days after hatching but slows up later to give a sigmoid growth curve (Fig. 19·1). No doubt a great many variations occur in nature and from place to place. Among some young predators and probably other birds too, a drop in weight takes place shortly before departure from the nest. This may be attributed to loss of fat (perhaps primarily), loss of the feather sheaths, and desiccation of the feather pulp. It may be that hardening of bone and tissue play a part in weight loss. It may also be that less feeding by adults occurs at this time, though it seems more probable that the loss in weight results from body changes not quickly equalized by food and moisture intake. Even in ordinary daily life, the weight of the nestling declines slightly during the night but increases again with daytime feeding.

The weight of the young bird may double in the first 2 days, sometimes for several such intervals. Data for the Field Sparrow illustrate this tendency, as well as the tendency for weight decline during the night (Table 19·1). The percentage of daily increase also illustrates growth rate. The successive percentage increase for the Great Tit from the first to the fourteenth day declined as follows (Gibb, 1950): 53, 50, 42, 33, 27, 21, 17, 13, 11, 8, 6, 4, 2, 1.

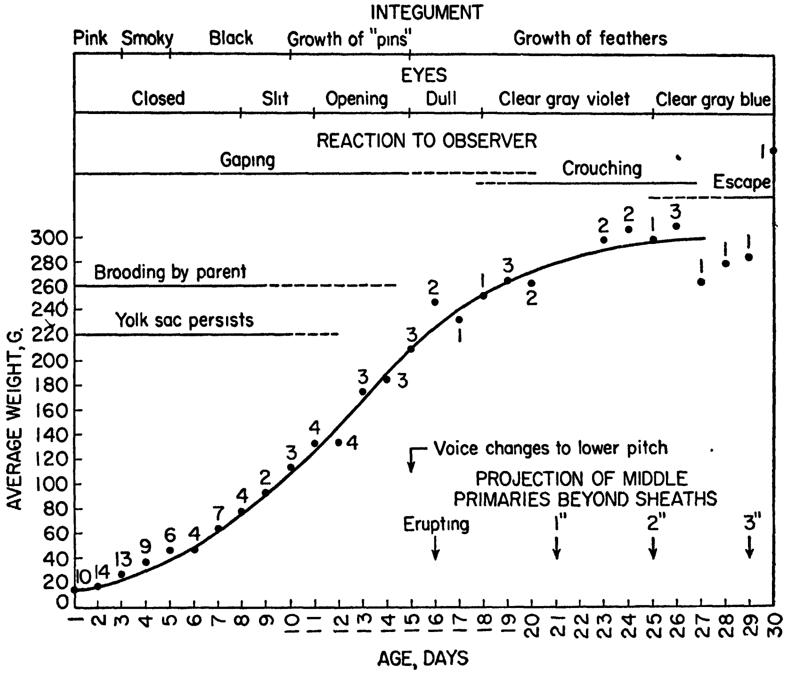

Fig. 19·1. *The development of nestling Crows. Figures above the data indicate number of birds measured. (After J. T. Emlen, Jr., "Notes on a Nesting Colony of Western Crows,"* Bird-Banding, *13(1942):143–154.)*

Table 19·1

Weight of Young Field Sparrows During First Seven Days

Age in Days	Weight in A.M. (Grams)	Weight in P.M. (Grams)
At hatching	1.72	1.71
1	2.75	2.75
2	3.51	3.74
3	5.25	5.66
4	6.99	7.24
5	8.79	8.86
6	9.70	9.75
7	10.17	10.40

Source: Lawrence H. Walkinshaw, "Nesting of the Field Sparrow and Survival of the Young," *Bird-Banding,* 10(1939):107–114, 149–157.

The various parts of the young bird's body grow at their own rates so that changes of the body itself from hatching to adulthood may be far from proportional. Comparison of hand-reared and nest-reared young show that the old birds are better parents than people. Hence, measurements taken from hand-reared young may not be indicative of true growth. The primary feathers of precocial birds develop at a comparatively faster rate than those of altricial young. Among birds in general, the wings develop faster than does the tail, which accounts for the bob-tailed look of fledglings during their early flying period. The weight may increase from hatching to fledging by ten to twenty times. Measurements of weight and other growth in the Scissor-tailed Flycatcher showed the following increases from hatching to 14 days of age (Fitch, 1950): weight 1000 per cent, wing extent 400 per cent, head length 343 per cent, bill length 300 per cent, middle toe length 288 per cent, tarsus length 278 per cent, and head width 100 per cent.

Action of Precocial Young. The precocial chick remains in the nest until the down has dried, by which time the bird has become strong enough to begin following the adult. The yolk from the egg supplies nourishment for a day or two longer than for altricial young. Within a day or two of its hatching, the young follows the adult from the nest, usually following the female (Grouse, Turkey, Duck), sometimes the male and female (Bob-white, Canada Goose, Whistling Swan), and rarely the male (Phalarope), according to species. Few broods return to the nest after having left it. Until they can fly into a tree for roosting like adults (page 208), the young of terrestrial birds may roost upon the ground. (Obviously, young of nonfliers like the Ostrich would not take to the trees.) Young water birds spend the night in the aquatic vegetation, on shore, on platforms of some kind, or in other selected places. Adults brood their precocial young for some time after hatching, often for several weeks.

The Impressionable Age. The young bird has a set of instincts for action (*innate behavior*) that unfold as the bird grows older. But a number of things can be acquired (*imprinting*), occasionally rather counter to or superimposed upon normal behavior (Thorpe, 1951). A regular sequence of instinctive actions develop as the young bird grows, beginning with first lifting its head and gaping for food (see Fig. 19·1). Later the young adds new action—begging, crouching, preening, signs of fear, bathing, calling. For each species, the sequence is about the same in all individuals.

The young may transfer a normal behavior procedure to some other object or action in captivity. Its importance in the life of a normal bird seems open to question. The parent association may be transferred to human beings or to an inanimate object. A bird fed from a pair of forceps may react to the forceps as to the normal parent. The appropriate reaction of the developing young may be stimulated by visual (e.g., the forceps), auditory (e.g., call of the parent), or tactile (e.g., touch of the parent) *releasers.* Such reactions are never to the environmental situation as a whole, only to parts of it (Tinbergen, 1948). But theories of instinctive behavior are open to many questions of both interpretation and neurology (Lehrman, 1953).

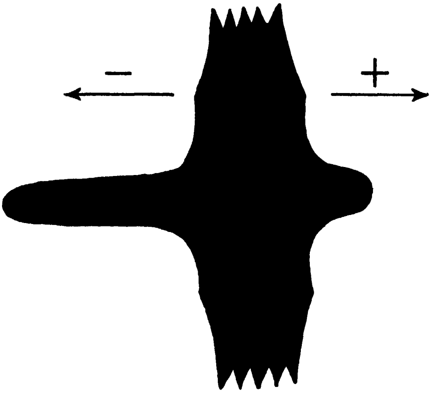

Fig. 19·2. *Cardboard dummy that releases positive escape reactions in Turkey chicks when sailed to the right (="Hawk") but not when sailed to the left (="Goose"). (After N. Tinbergen, "Social Releasers and the Experimental Method Required for Their Study,"* Wilson Bulletin, *60 (1948):6–51.)*

The reactions of young to prey have been tested experimentally by means of cardboard cut-outs forming a silhouette. When a dummy (Fig. 19·2) was sailed over young Turkeys, it caused different reactions, depending upon the direction of movement of the dummy. The short-necked appearance of the dummy when moving in one direction seemed to signal *predator,* the long-necked appearance the other way seemed to signal *Goose* or other nonpredator. A series of cutout models released escape reactions only when of a short-necked shape (Fig. 19·3). Adult and young have rather fixed and definite reactions to releasers, though those of the young may differ from those of the adult. A young altricial bird will crouch in fear, but a precocial bird will "freeze"; in many ways, however, the two actions are similar. Later the precocial young may react by escape.

Fig. 19·4 shows characteristic attitudes of an adult Song Sparrow under different circumstances. The nestling may not respond to some of these attitudes and to others it may respond only by crouching. Other species have various attitudes, some similar to those of the Song Sparrow, others markedly different.

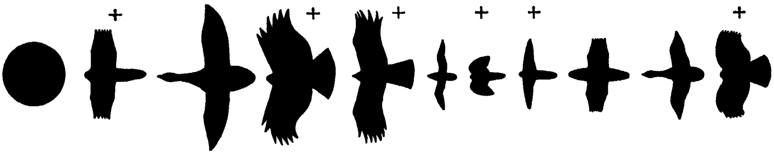

Fig. 19·3. *Cardboard models used to test reactions of birds. Only the short-necked models (marked +) stimulated escape reactions. (After N. Tinbergen, "Social Releasers and the Experimental Method Required for Their Study,"* Wilson Bulletin, *60(1948):6–51.)*

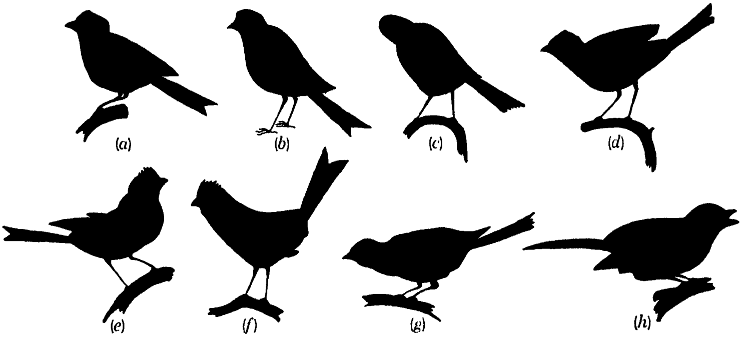

Fig. 19·4. *Attitudes of a Song Sparrow in alarm, fear, and fright: (a) Unalarmed, (b) alert, (c) turning head to look, (d, e) alarm with flipping of wings and tail, (f) strong alarm, (g) fear, (h) fright (with panting). (After Margaret Morse Nice and Joost Ter Pelkwyk, "Enemy Recognition by the Song Sparrow,* Auk, *58(1941):195–214.)*

PARENTAL CARE

Care of Precocial Young. The young feed some for themselves as the brood wanders about. The parent or parents, however, find most of the food for the first few days and much of it for an indefinite time thereafter. The young recognize many kinds of foods instinctively and avoid others in the same way. While many acts of the young indicate instinctive controls, others are not so readily classified because the adult is along as a model. In general, birds hatched in an incubator and later raised in a brooder will grow up to act like any other birds of the species, though some readjustment of life may be in order as they mature. Yet the appearance of many behavior characteristics may be delayed. Young are likely to dust earlier in the wild with the brood than when raised artificially. Some species have difficulty in recognizing surface water for the first time, though most precocial young recognize water drops that simulate dew drops, evidently an instinctive response.

Upon approach of any enemy, the precocial young freeze during the first few days but scatter later when they can fly. The warning call of the adult becomes recognized quickly, though whether by instinct, by learning, or by a combination of instinct and learning has not been established. The adult with a brood of young may feign injury, though sometimes it will attack an intruder, often a large one. Upon the passing of danger, the old bird brings the brood together by a special rallying call. During the process of assembling, much calling by the adult and peeping by the young may take place.

The precocial young of aquatic birds leave the nest and swim about in the water. Some can dive easily at the approach of danger, but many young may freeze when small and escape by flight or swimming when older and larger. Many species, perhaps most, use concealment more than any other way of escaping danger.

The number in the brood of precocial birds declines progressively during the season because of mortality. Some lost or strayed young will join other broods and some recombining occurs among several species, especially where broods are concentrated. The average brood of the Blue Grouse drops from about four or five in June and early July to about two in early August; combining of broods late in August may raise the average again (Wing, Beer, and Tidyman, 1944). The average numbers in Turkey broods from May to October illustrate a steady decline, greatest when the young are smallest: May, 10.7; June, 8.2; August, 7.8; September, 6.9; and October, 6.7 (Bailey *et al.*, 1948).

Protection in the Nest. Upon hatching and for some days thereafter, the old birds brood the newly hatched nestlings to protect them from cold or sun. A record of an observer's visits to a Field Sparrow nest showed brooding (by the female) during all the visits for 2 days after hatching, 87.5 per cent the third day, 60 per cent the fourth, 20 per cent the sixth, and none thereafter; the young were brooded at night 100 per cent of the time until 6 days old (Walkinshaw, 1939). Similar variation in brooding as the young become older is the rule with most other altricial species, just as incubation may have variations (page 371). A comparison of the attentive behavior of eight species of New World Warblers during the first 4 days after hatching showed brooding periods to average from 15 to 25 minutes in length and the time off the nest to average from 4 to 15 minutes (Kendeigh, 1945).

Among a number of species, one parent, usually the female, stays on guard duty for the first days while the other is away, so that they leave the young exposed not at all or momentarily at most. Often complicated signals mark the change of watch at the nest, though sometimes the birds change places with little ceremony. The mated Yellow-eyed Penguins, which recognize each other on sight and sometimes by voice when out at night, put on a rather violent welcoming ceremony, bowing (usually with a burst of notes), and with court-

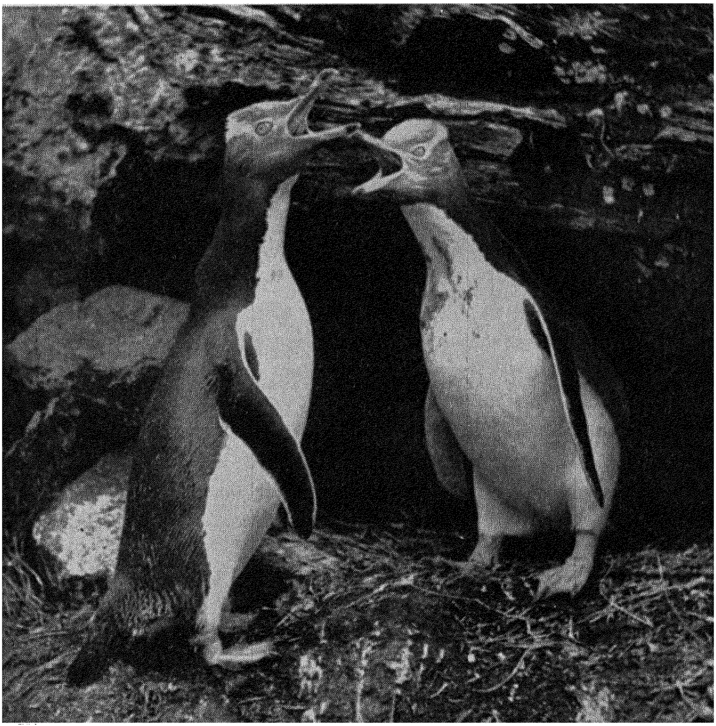

Fig. 19•5. *The culminating point in the "welcome ceremony" of the Yellow-eyed Penguin. The male (left) has just returned and the female is at the edge of the nest, the two 8-day-old chicks behind her. (By permission from* Sexual Behavior in Penguins, *by L. E. Richdale. Copyright, 1951, University of Kansas Press, Lawrence, Kan.)*

ship behavior (Fig. 19·5). In a few species that travel far for feeding (e.g., Adélie Penguin), some adults remain as guards or "nursemaids" for the half-grown young of several different nests.

When an intruder disturbs or endangers the nest or young, some birds slip away quietly and unobtrusively. Some may attack the intruder, a habit famed in the Eastern Kingbird. Often newspapers report seemingly unprovoked attacks upon passersby from Screech Owls, American Robins, and other birds. The probable explanation is presence of young or a nest near by. Other birds may fly about in the bushes or trees, often at close quarters. Occasionally, a bird will engage in a substitute attack (displacement action) on some object. The male American Redstart shows more fear of approaching an intruder than the female. (In most species, the female is the more aggressive in nest defense.) But he may transfer his attack to her as she flutters about the intruder. In some cases, attack, usually by the male, may be transferred to an inanimate object.

Feeding the Young. The growing young require a seemingly prodigious amount of food, they develop so rapidly. The young have a high protein demand, higher than that for adults. Because animal foods tend to be richer in protein (and moisture), more concentrated, and probably more easily made ready for assimilation in the body, the parents of many birds, even seed-eaters or herbivorous ones like the Grouse, feed animal foods to their young.

Most birds bring food to the nest in the bill, but some carry it in a gular pouch, crop, or sometimes stomach. Predatory birds use the feet ("talons"). The parents break up large pieces of food but feed small things whole. The Pelican opens its beak and lets the young rummage for food. The Bittern regurgitates food directly into the mouth of the young, but others may feed it themselves after regurgitation. Obviously, such food may be in various stages of digestion. It is said that as the young grow older, the food is fed in a less digested state. Rather unusual among Passerines is the mouth sac of the Gray-crowned Rosy Finch of the Alpine zone; it may nest among the rocks and have to forage far for insects, which it can bring in numbers by means of its special sac (Fig. 19·6). The Pine Grosbeak has an identical arrangement (French, 1954).

The rate at which the parents feed the young depends upon the habits of the species, the growth of the young, the success of the adults in foraging, and whether one parent or both do the feeding. Sample hourly rates reported for the active part of the feeding periods show a wide divergence: American Goldfinch 2.0, American Crow 3.0, Ruby-throated Hummingbird 5.0, Ovenbird 5.3, Scissor-tailed Flycatcher 6.7, Yellow-headed Blackbird 9.6.

More active feeding has been reported, and it may be that among some species, much greater activity is the case. The House Wren established a record of 77.3 feedings per hour for a day of nearly 16 hours. Feeding visits numbering from 400 to 600 a day have been reported for various other Passerine birds. But large predators feed only a few times a day, sometimes only once. The Gray-crowned Rosy Finch, because of its pouch (Fig. 19·6) brings food at intervals of about three-quarters of an hour; the number of visits in consequence is about as few per day as those made by any Passerine. Petrels, Shearwaters, and some other sea birds feed the young about once a day. The Manx Shearwater has been reported to range 600 miles at sea from its nest burrow while searching for food. The robust nestlings may go unfed for several days during poor food-gathering weather but are able to withstand considerable fasting and yet recover —lengths without food that would be fatal to the young of almost any other species. The young of the Sooty Shearwater spend about 14 weeks ashore and may also go unfed for various intervals of time. During these fasts, the body weight drops but subsequent feeding brings quick recovery. One observed young in a colony went unfed for 10 days and recovered. Evidently the recovery capacity of these young has evolved to balance the variable feeding success of the parents during stormy weather at sea.

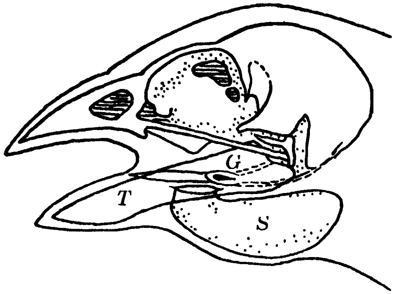

Fig. 19·6. *Skull of a female Rosy Finch to show the left mouth-sac (S) with opening in the floor of the mouth lateral to the tongue (T) and glottis (G). (After Alden H. Miller, "The Buccal Food-Carrying Pouches of the Rosy Finch,"* Condor, *43(1941):72–73.)*

Nest Sanitation. The nestlings of common songbirds defecate several times a day, sometimes two or three times an hour. A mucous coating makes a sort of bag, which the adult carries off and drops. For the first few days, the adult may swallow the feces, but later usually carries the fecal sack a number of rods away before dropping it. Young of predators and most other large birds defecate over the edge of the nest; the young of a few Passerine birds (such as the American Goldfinch and Barn Swallow) do likewise.

Length of Nestling Period. The nestling period for practical purposes is the time between hatching and departure from the nest. The nestling period of small altricial birds about equals the incubation period. But a few birds show regular variations. Cavity-nesters like the Woodpeckers and long-winged flyers like the Swifts and Swallows tend to have longer nestling than incubation periods. The young of these birds are mature enough when leaving the nest so that most may launch out and after a few preliminary wobbles take off in flight nearly as well as their parents. Bank-burrowers (e.g., Kingfisher, Motmots, Jacamars, and some Swallows) have both long incubation periods and long nestling periods. The nestling period of tropical young tends to be longer than that of their relatives in higher latitudes, which length also parallels differences in incubation periods. Although migration, nest building, and other habits of the adults accelerate poleward, it is not known whether this happens in the growth of the young. Some Arctic studies have tended to show that it may for some species, but the evidence is fragmentary.

Some birds have very long nestling periods, especially the larger predatory birds and their allies. Young of a large Hawk may spend 8 weeks in the nest. The young Manx Shearwater spends 6 weeks and the Sooty Shearwater 14 weeks in the nest. The Royal Albatross takes 7 to 8 months for this period. The little Field Sparrow, on the other hand, may leave the nest at 1 week of age, though its incubation period is 11 days. The Sooty Shearwater, however, has an 8-week incubation period and a 14-week nestling time.

LIFE OUT OF THE NEST

Leaving the Nest. A nestling becomes a *fledgling* as soon as it leaves the nest of its own accord. It remains a fledgling until it can fly with ease. (Obviously, some indefiniteness occurs in the use of terms.) The young often indicates the approach of its first departure from the nest by perching on the edge of the nest for a few hours or a few days before leaving. Some young may climb out onto the surrounding branches for several days but return to the nest at night. Young of some ground-nesting birds like the American Marsh Harrier or Black Vulture may move about in the weeds or bushes in the vicinity of the nest during the late nestling stage.

Just as laying and hatching occur largely in the morning, so also does departure from the nest. Some young depart by creeping out onto the limbs and slowly keeping on going. Some marsh birds (like the Yellow-headed Blackbird) leave the nest and creep around in the vegetation for several days and even longer before they can fly. But some young get up, stretch their wings, and leave by flying, often coming to earth after a short distance and then hopping into a hiding place. Nestlings within a few days of normal departure may leave unceremoniously at the advent of danger, even though unable to fly. Many of the baby American Robins hopping about on lawns thus may have left prematurely. Young of songbirds dumped out of the nest more than 2 or 3 days prior to the normal departure stage are hardly likely to survive.

Feigning Injury. Ornithologists differ in interpreting the meaning of injury feigning by birds. Many see it as protective behavior associated with the nest or young and occasionally otherwise (Fig. 7·18). Others give the bird less credit for its action and interpret it as a behavior resulting from psychological conflict in the bird, probably from anxiety or fear. This view considers injury feigning as related to or actually a form of catalepsy. Birds nesting on or near the ground are the chief performers, but seldom other than in connection with nests or broods (Armstrong, 1947). Experienced field ornithologists differ with the view of injury feigning as a cataleptic condition, at least in many performers. The evident awareness of the acting bird to the intruder and the apparent governing of its acts accordingly show more conscious decision by the bird than mere catalepsy would involve. The bird's actions appear rather well under control and the performer is not often captured by enemies. Injury feigning may be a form of *diversionary display* arising from displacement of components of other behavior patterns, particularly of threat and courtship display. These may have become established as a new behavior pattern of survival value (Armstrong, 1949). The simplest explanation of injury feigning (and therefore the most reasonable one) is that it is merely a highly developed form of conspicuous departure from the nest (Skutch, 1955).

Postnestling Care of Altricial Young. The parents ordinarily continue feeding the young for some time after they leave the nest; seldom, however, are they brooded. Often the parent "leads" the newly departed young to a place of safety. By means of calls, the hungry young makes known its position to the adults, which by that means locate scattered birds to feed them. In some cases and among some species, the male takes care of the brood while the female lays another set of eggs. Among others, the male may stay for a time but leave most of the care to the female. Obviously, this may delay or prohibit renesting.

The length of time during which the parents feed the young seems to vary greatly. Full-sized young have been noted begging for food weeks after leaving the nest. But others seem able to shift for themselves rather easily. The young often remain in the home vicinity for a while before wandering off. Among many of the larger birds, a northward wandering has been revealed by banding (see Chapter 16); but among others, wandering may be an early drift toward winter quarters.

The young of earlier broods in several species have been observed to help with feeding the young of later broods, but how regular or significant is unknown. It may actually represent a "premature act" of the young, just as the young may exhibit other premature acts during the fall and winter (page 331). Sometimes there are helpers at the nest (Skutch, 1935).

Mortality of Young. The steady decline in brood size measures the mortality of the young in precocial birds, subject to wandering and recombining of brood members. The heaviest mortality of precocial and altricial birds may occur when the young leave the nest, but the crucial hatching period may witness a heavy loss also. Mortality varies from local catastrophe, when it could reach 100 per cent, to very low losses. Probably a mortality of 40 to 75 per cent of the young is the most usual range. But complications in gathering data on the success of young after they have left the nest make all such estimates difficult. The actual success of nestlings (from hatching to departure) is often high, locally reaching 90 per cent. Various estimates of losses of nestlings have been reported; for example, Yellow-headed Blackbird 72 per cent, Ovenbird 56 per cent, Eastern Bluebird 51 per cent, and Song Sparrow 40 per cent. Some estimates have indicated that fully 75 per cent of the young hatched do not survive until the first winter. Losses after that have been variously estimated up to about 25 per cent by the beginning of the next breeding season (see also Chapter 14).

SUGGESTED READING

*ALLEN, ARTHUR A., *The Book of Bird Life.* New York: D. Van Nostrand Co., Inc., 1930.

*ARMSTRONG, EDWARD A., *Bird Life.* New York: Oxford University Press, 1950.

*BENT, ARTHUR CLEVELAND, *Life Histories of North American Birds.* U. S. National Museum Bulletins, 1919–.

HERRICK, FRANCIS HOBART, *Wild Birds at Home.* New York: Appleton-Century-Crofts, Inc., 1935.

HUXLEY, J. S., *Problems of Relative Growth.* London: Methuen & Co., 1932.

KENDEIGH, S. CHARLES, *Parental Care and Its Evolution in Birds.* Illinois Biological Monographs, 22(1952):1–356.

*LEHRMAN, DANIEL S., "A Critique of Konrad Lorenz's Theory of Instinctive Behavior," *Quarterly Review of Biology*, 28(1953):337–363.

NICE, MARGARET MORSE, *Studies in the Life History of the Song Sparrow*. Transactions of the Linnean Society of New York, 4(1937):1–247, 6(1943):1–328.

*NICE, MARGARET MORSE, *The Watcher at the Nest*. New York: The Macmillan Co., 1939.

*TINBERGEN, N., "Social Releasers and the Experimental Method Required for Their Study," *Wilson Bulletin*, 60(1938):6–51.

*TINBERGEN, N., *The Study of Instinct*. Oxford, England: Clarendon Press, 1951.

20

Heredity in the Bird

Other than for the adult characters that mark the parents and the juvenile ones that mark the young, most parents and offspring appear much alike to our eyes. Differences in characters between the sexes may be greater than age characters between the respective adults and young. Each young bird inherits its genetic composition from the genetic make-up of its parents, just as the parents received theirs in turn from their parents. The study of inheritance is called *genetics*, but we know little of heredity in wild birds. It may be assumed, however, that it does not differ significantly from that known for domestic and experimental animals. But survival in the wild would leave few recipients of unfavorable or weakened hereditary characters to be seen. Proportions in the wild may be somewhat distorted as compared to experimental animals.

Inherited Characters. The units believed to control the inheritance of any feature are the *genes*, carried in *chromosomes* and transmitted through the germ cells. Each gene or pair of genes in homologous chromosomes controls the expression of one or more hereditary *characters*—subject many times to interaction with other genes, with the body, and with the environment. Though a gene controls an inherited character, characters may be complex and influenced by several genes (multiple factors). Because an individual receives its chromosomal make-up from its parents, it normally gets from each parent a gene affecting the characters of that parent. The genetic constitution of a bird forms its *genotype*; the expression of this is the *phenotype*.

One gene may *dominate* over its corresponding gene and produce an individual somatically identical with one that has received identical genes from each parent. The one gene is called *dominant* and the other *recessive*. This condition of differing genes in a pair makes the individual *heterozygous*, that for like genes makes its bearer *homozygous*. A widely used example of this occurs in the Domestic Chicken in which the gene for rose comb (denoted by *R*) dominates over the gene for single comb (denoted by *r*). The heterozygous bird (*Rr*) appears identical with the homozygous dominant form (*RR*)—both bear rose combs. But the homozygous recessive form (*rr*) differs from both and has a single comb. All offspring of two single-comb parents will have single combs also, but all offspring of two homozygous rose-comb parents will have rose combs. The offspring of two heterozygous parents (themselves rose comb) will be both rose-comb and single-comb birds in the ratio of three to one. The three-fourths of the offspring receiving *R* will have rose combs; the one-fourth receiving recessive genes from both parents (*rr*) will have a single comb.

Characters influenced by the action of more than one gene will be inherited differently. Thus, if two genes supplement the action of each other, the offspring may differ from either parent accordingly. Some characters, such as those of color and size, may be the result of several genes having a cumulative action. If a sex chromosome carries the gene for a character, the character is *sex-linked*. Two genes on the same chromosome show *linkage*. But if a chromosome exchanges homologous parts with its fellow at the time of formation of germ cells, *crossing-over* occurs.

Inheritance in the Wild. Because we know so little of inheritance among wild birds, it is difficult to find examples in nature of even simple dominance of a normal character over the recessive. *Mutations*, however, are likely to be recessive, but mutations in the wild are rather unknown and their inheritance factors are less known (page 395). *Hybrids* between species (or races) give some indication of the inheritance of interspecific dominant and recessive characters. In crosses between Red-shafted and Yellow-shafted Flickers, the yellow of the wing and tail feathers appears to be dominant and the red recessive (Deakin, 1936). There is some reason also to believe that the red of the Red-shafted may be a multiple-factor character. Other Yellow-shafted Flicker characters, except the fawn color of the throat, appear likewise to be dominant over those of the Red-shafted.

Crosses between members of the Grouse family (Tetraonidae) indicate that if one species possesses larger amounts of feathering on the legs, this condition will be dominant over less feathering. Color in the plumage of birds may be dominant over white in some cases and recessive in others. In hybrids between Fringillids, streaking seems dominant over plain colors. Among hybrids of the Gray-headed Junco, Western (Oregon) Junco, and Pink-sided Junco, red appears dominant over yellow when the Western Junco crosses with the Gray-headed Junco. The yellow dominates over the red, however, in crosses of the Gray-headed Junco with the Pink-sided Junco (Miller, 1939).

Crosses between the Golden-winged Warblers and Blue-winged Warblers occur in parts of eastern United States and Canada. Hybrids are known as Brewster Warbler and Lawrence Warbler, depending upon which form they take. The former looks much like a Blue-winged Warbler with largely white underparts in place of yellow, while the rarer Lawrence Warbler appears somewhat like a Golden-winged Warbler with yellow underparts in place of white. The Golden-winged when of the pure type appears to be homozygous for the dominant white underparts (dominant over the yellow of the Blue-winged Warbler), and recessive for the black throat when it hybridizes with the Blue-winged Warbler. The Blue-winged when of the pure type, on the other hand, appears homozygous for the recessive yellow and for the dominant plain throat (dominant over black) when it crosses with the Golden-winged Warbler (Pough, 1946). Because the Brewster Warbler shows the respective dominant characters in the hybridization, it may be heterozygous or homozygous for them. The mating of a heterozygous Brewster Warbler with either a heterozygous Golden-winged type or heterozygous Blue-winged type can give a Lawrence Warbler (the recessive). Since a Brewster may be heterozygous as well as homozygous for the dominant characters while a Lawrence Warbler must be homozygous for the recessive ones, the greater number of Brewster Warblers in the wild is evident.

The single yellow wing bar of the Golden-winged Warbler is reported to be incompletely dominant over the double white wing bar of the Blue-winged Warbler and linked with the white underparts. In the same way, white underparts appear to be incompletely dominant also over the yellow. Several variations from the "normal" Brewster and Lawrence types have been noted, all of which may result from this incomplete dominance and perhaps crossing-over also (Parkes, 1951).

Two unusual facts have been uncovered about the hybridizing of the two species: (1) Though they occur frequently where the two species overlap, few specimens were known before their published descriptions in 1874. That they evidence greater abundance since 1874 than formerly cannot be accounted for entirely by the greater interest and zeal of bird people. This has suggested the postulate that the ecological and geographical overlap making hybridization possible has been brought about by man's disturbance of the biota in their joint range. (2) Few cases (none completely free from question) of hybrid-hybrid matings are known, which seems to indicate some preferential factor in operation favoring *back-cross matings* between the hybrids and a parental phenotype.

"Left-handedness" has been reported in Parrots and may occur in other birds, and testing for it seems desirable. Twenty Parrots of sixteen forms averaged 72.2 per cent "left-handed" in 380 test observations. Eleven showed 75 per cent or more preference in holding food with the left foot, five showed 100 per cent preference (Friedmann and Davis, 1938). While nothing is known of inheritance of such a character, variation among species would indicate its inheritable nature.

Many of the morphological, physiological, and psychological characters of a genetic nature may be influenced or controlled in part by inheritable variations in the nervous and endocrine systems controlling them, as well as by the gene structure. Studies of the inheritance of "wildness" in the Turkey show significant differences between the adrenal gland and pituitary gland weights of native and domestic types (Leopold, 1944). The adrenal weight of the native type averaged about 0.03 per cent of the body weight, more than twice that of the domestic type. The pituitary of the native type averaged about 50 per cent greater than that of the domestic type. Since there are marked differences in some manifestations dependent upon endocrine glands, the key to the difference in inheritance may be in the glands themselves. The brain development, for example, is related to adrenal secretions, and the wild type with the larger adrenals has a larger brain than the domestic type. It seems clear that consciously or unconsciously, the less wild and more tractable Turkeys have been selected by man.

Sex Characters. Secondary sexual characters in the form of head adornments of wild and domestic types of Turkey gobblers respond to hormones also. First-year wild gobblers have little such development in marked contrast to older birds and to first-year domestic gobblers. Crosses between the wild and domestic birds result in an intermediate condition (Fig. 20·1). The difference seems associated with inheritable differences in activity of the endocrine glands, specifically the pituitary that controls, through gonadotropins, elaboration of sex hormones by the gonads.

Because some characters are sex-linked, the gene for that character is carried by the sex chromosomes. Studies of bird and reptile chromosomes show that the male has two similar sex chromosomes (ZZ), the female either two differing ones (ZW) or only one (ZO), so that

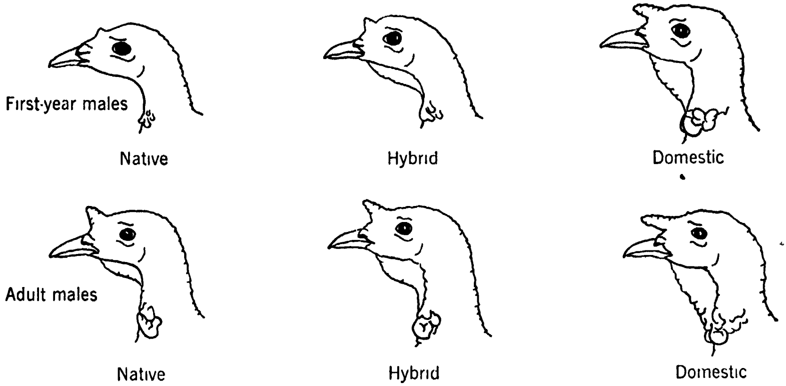

Fig. 20 • 1. *Comparative development of male secondary characters on the head of native, hybrid, and domestic Turkeys in winter. (After A. Starker Leopold, "The Nature of Heritable Wildness in Turkeys,"* Condor, *46(1944):133–197.)*

the condition in birds and reptiles is the opposite of that in mammals. The female bird is the *heterogametic* sex, the male the *homogametic* sex. Although all families and orders of birds and reptiles have not been studied for sex chromosomes, expectations are that the heterogametic condition in the female is universal among them.

In addition to sex-linked characters, there occur also *sex-limited* ones. The male plumage of many species, for example, is not a character carried in the sex chromosomes but is a character determined by the presence or absence of sex hormones. The removal of ovaries in birds or their loss by disease will cause the bird to take on male characteristics of plumage, voice, and nervous system. Evidently the ovarian hormones *inhibit* the male plumage. In the same way, loss of the male hormones, as by castration, disease, or age, will cause the male bird to take on a more neutral plumage and action than previously. In the light of our present knowledge, it is difficult to distinguish between sex-linked characters (such as the size of males and females in some species) and sex-limited or sex-influenced ones (such as the male appearance of the individual). Yet the color and other sexually dimorphic characters of the Cowbird and Brewer Blackbird are genetically determined and not under the control of sex hormones (Stanley, 1941). The fact that the female Phalaropes and some females of predaceous birds tend to be larger than the males may indicate a sex variation perhaps differently inherited.

Sex Determination. It is customary to say that in heterogametic animals, sex determination occurs at the moment of fertilization. But it is sometimes said that among animals like the bird in which the male is the homogametic sex and all sperm alike, sex determination takes place a few moments prior to the fertilization when the first polar body leaves the oocyte ahead of the rupturing of the ovarian follicle to release the oocyte. If the released oocyte itself carries the sex chromosomes, the egg will give rise to a male individual, but if the sex chromosome passes to the polar body, a female will result.

Just how the sex chromosome gives rise to a male is not clear, but presumably it carries potentialities for maleness that modify those of the *autosomes* so that maleness predominates and a male bird results. The male shows a higher metabolic rate than the female, which seems an associate of maleness.

The sex ratio in Chickens appears to change with increased production of eggs so that later eggs produce more males as the energy resources of the laying bird become depleted (Romanoff and Romanoff, 1949). The sex ratio of 589 first-laid of *paired* Rock Dove eggs was 103 (103:100) and for 545 second-laid of paired eggs, 113 (113:100) (Cole and Kirkpatrick, 1915).

The ratio of male and female individuals at fertilization is referred to as the *primary sex ratio* (Chapter 8). On theoretical grounds, this should always be even—that is, equal numbers of ovums with and without the sex chromosomes are fertilized. So far as is known, birds produce both types of gametes (Z and *W*, sometimes Z and *O*) in equal numbers. There is no evidence that one type of ovum attracts sperm more than the other, though such could conceivably occur.

Lethal Characters. Experimental crossing of Domestic Chickens has demonstrated the existence of *lethal characters* and that individuals having them die in the embryonic state, seldom living after hatching. The genes for them may be carried in the sex chromosomes, so that the lethal characters appear in one sex more than in the other or exclusively in one sex. Some of the failures of eggs to hatch in the nests of wild birds might very well be caused by lethal characters, and examination of such eggs would presumably clarify this point.

Mutations. Gene changes that result in new inheritable variations have been termed *mutations.* The mutation rate seems to be low but variable among species (as should be expected). Mutations are not well known for wild animals, in part because mutations tend to be recessive to the normal and in part because they tend to be of less survival value to the individual. In addition, it may be that mutations are but part of an upset in the body complex (Lee and Keeler, 1951).

A red condition, possibly a mutation, appeared among Bob-whites in the Southeast and persisted in the wild for some time but slowly disappeared (page 126). Studies and experimental breeding of captured birds established that the birds with red plumage were distinctly weaker, less thrifty, and less vigorous than the normal. The red condition was apparently an incomplete dominant (Cole, Stoddard, and Komarek, 1949). In general, however, normal red phases in nature (page 126) do not mean weaker individuals, at least so far as known to biologists (as in Screech Owls, Pygmy Owls, and Ruffed Grouse), which suggests the possibility that red mutations might eventually become normal colors if the vigor of the bird should be unimpaired or re-established.

Albinistic characters seem to be inherited as simple recessives. Yet normal white, as distinguished from albinism, may be dominant to color. An 18-year series of observations of a flock of House Sparrows in Washington, D. C., is interesting in showing persistence of albinism. It is also interesting in showing how easy it is for alert ornithologists to discover new things in the bird world. The flock contained many partially albinistic members through the years, and they showed lack of vigor as compared to other flocks of Sparrows (Davis, 1947). The persistence of white is of greatest importance perhaps as showing the flock persistence through several generations during which individuals were hatched and died.

Melanism (and occasionally another color) appears as a normal, sometimes dominant, color phase in several species of birds (page 126). It may also occur as a mutation of part or all of the plumage.

Dilution of color probably constitutes a form of partial albinism. Birds are seen occasionally that have a paler color than the normal, such as a paler blue condition in several of the Jays, that suggests decrease of the blue (a structural color, page 124) by increase of the white component in the color. The *intensification* of color appears also in some birds, which suggests a reduction in the white of the color or perhaps increase of melanins. The dilution and intensification in the plumage may occur by change in the white, just as a painter makes shades by adding or reducing white.

Darkening of the plumage color appears also, and may indicate partial melanism, insufficient to show as deep brown or black. Melanism and albinism appear more often or perhaps are recognized more often in birds respectively of predominantly grayish or blackish plumage. Other changes also probably sometimes mutational in origin are the yellowish appearance of normally greenish plumages of some Parrots (page 126). Most of the important characters of animals seem to result from multiple gene action, so that this yellowish appearance may be a mutation in one or more of the genes involved. In the South American genus *Buarremon,* a mutation of the dark pectoral band is postulated as giving rise to the species *Buarremon inornatus* from *Buarremon brunneinucha*. The former now occupies a restricted range in the subtropical zone of western Ecuador, while its parent species ranges widely.

A mutation to be inherited must be in the genes of the germ cells; mutations in the somatic cells would not be inherited. Our best evidence of mutation in birds appears in Domestic Chickens and Domestic Pigeons. Many bizarre varieties and individuals have resulted from mutations and recombinations, some of them markedly different from anything in the ancestral Jungle Fowl or Rock Dove.

Geographical and Ecological Variations in Inheritance. While we recognize many geographical variations, some over large areas (such as the paler plumage of desert birds or darker plumage of humid region ones), some over small areas (such as the appearance of white feathers in the birds of some localities), we are unable to describe clearly their genetics. Yet a genetic base seems certain. The many geographical variations recognized as subspecies attest to probable inheritance of characters on a regional basis. Ecological variations also show probable regional inheritance, as in the reported possession of longer wings by Starlings in the windy Faroes as compared to the less windy mainland. The increased size of birds in the cold regions and decreased size in the warmer ones in accordance with the *Bergmann Rule* (Chapter 10) likewise indicates ecological and geographical variation of an inherited nature.

Segregation of plumage characters in Old and New World groups of species in the genus *Columba* shows that genes affecting plumage color are distributed in significantly different frequencies (Fig. 20·2). Antigens in the blood also show geographical segregation.

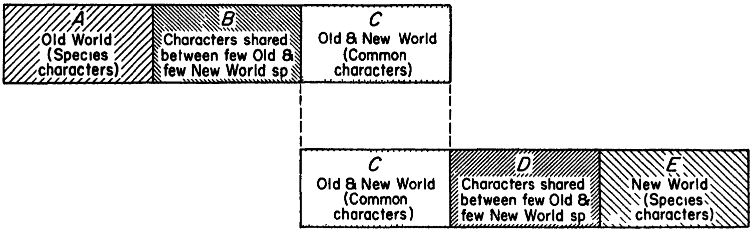

Fig. 20·2. *Categories of plumage characters in the genus* Columba. *(A) exclusive to Old World birds, (B) mostly of Old World birds, (C) common to both Old and New World birds, (D) mostly of New World birds, (E) exclusive to New World birds. (After Russell W. Cumley and Leon J. Cole, "Differentiation of Old and New World Species of the Genus* Columba," American Naturalist, *76(1942):570–581.)*

Aberrant Forms in Nature. Many strange or grotesque individuals have been reported by collectors, bird banders, and others. Crossing of the mandibles or greater length than normal has been reported many times. How many of these are inherited as mutations or how many have resulted from deforming accidents or some other abnormality, we do not know. But the presence of similar conditions in the bills of domestic poultry and the hereditary nature of some of them suggests the possibility that some could be inheritable in the wild. Abnormalities of the feet occur, but most of these may be the result of disease or accident. Major abnormalities of the wings most likely would have an unfavorable survival value and the malformed individual thereupon be eliminated. This may account for the rarity of wing abnormalities compared to those of the feet or bills. Yet many injured birds recover (Chapter 21).

Natural Hybrids. In addition to the hybrids cited earlier in this chapter, many apparent hybrid individuals have been found. The Blue and Snow Geese have been reported to cross freely in the northern Hudson's Bay region; but the explanation may be that the Blue Goose is a geographically restricted color phase of the Lesser Snow Goose.

Hybrids occur between various Ducks (and sometimes between Geese) in Waterfowl marshes, perhaps because of the pressure for space and mates within the restricted area of the marsh habitat. The Mallard is especially likely to cross with other Ducks; so also is the Pintail. In general, hybridization occurs most frequently between closely related or ecologically closely associated species, particularly where the two sexes do not form a pair-bond of any duration or care for the young jointly. Presumably, the complex courtship and family procedures (with resulting lengthy mated life) together militate against the crossing of two dissimilar individuals, as in two birds of different species. Though nearly all orders have shown at least one hybrid, judging by numbers reported, they occur most often in the Ducks, gallinaceous birds, and Passerines. They occur less often among Pigeons, Hummingbirds, Hawks, and Woodpeckers.

Use of Birds in Genetic Studies. Geneticists and animal breeders have found the Domestic Chicken and Domestic Pigeon particularly plastic in their hands. Though the best evidence indicates that these two came from the Jungle Fowl and Rock Dove, respectively, the probabilities are always present that man has added a sprinkling of genes from other species during the long history of domestication. The Canary has also proved rather amenable to breeding and is frequently used in the genetics aviary. Other domestic birds have proved less pliable in the hands of the breeder, though several breeds of some have been developed, either by modern or ancient man.

Geneticists use the Pigeon and Chicken for breeding experiments, for which they have served well. About seventy-five characters, each determined by a single gene, have been identified or their inheritance determined in the Chicken. A large number of quantitative characters, such as of size, weight, age of laying, number of eggs, and the like, have been studied genetically in the Chicken and Pigeon (Snyder, 1951). Many multiple characters are likewise known. Thus, the normal dark color of the Dove, *Streptopetia chinensis*, forms a triple allelomorph with the sex-linked "blend" and "white" of the captive Ring Dove (Cole, 1930).

SUGGESTED READING

DOBZHANSKY, T., *Genetics and the Origin of Species.* New York: Columbia University Press, 1941.

FISHER, R. A., *The Genetical Theory of Natural Selection.* Oxford, England: Clarendon Press, 1930.

HUTT, F. B., *Genetics of the Fowl.* New York: McGraw-Hill Book Co., Inc., 1949.

MAYR, ERNST, *Systematics and the Origin of Species.* New York: Columbia University Press, 1942.

ROMANOFF, ALEXIS, and ANASTASIA J. ROMANOFF, *The Avian Egg.* New York: John Wiley & Sons, Inc., 1949.

SINNOTT, E. W., L. C. DUNN, and T. DOBZHANSKY, *Principles of Genetics.* New York: McGraw-Hill Book Co., Inc., 1950.

*SNYDER, LAURENCE H., *Principles of Heredity.* Boston: D. C. Heath & Co., 1951.

21

Health in Wild Birds

Because birds like other free-living organisms must be their own providers, the price of body malfunctioning is likely to be high. The kinds of malfunction are many (e.g., endocrinal and nutritional disturbances, injuries, and environmental strains). Diseases of birds, especially the parasites to which birds are hosts, have been frequently reported. Diseases in wild birds, so far as known, seldom limit the populations except possibly locally, though widespread disease in birds could conceivably cause extensive mortality. Heavy losses from botulism in Waterfowl areas of western North America have occurred. Malfunction of the body through external strains—such as of weather or diet—is a more likely health condition affecting bird numbers in cooler or drier regions. In general, diseases become more important in the warmer and wetter regions, climate in the cooler and drier ones. Malfunctions of the body arise from causes that may be listed under five headings:

Poor living habits (poor habitat, fatigue, disturbance)
Disease organisms (parasites, bacteria, viruses, rickettsias, fungi)
Toxins and poisons
Dietary deficiencies (lack of vitamins, minerals, water)
Injuries

POOR LIVING HABITS

Once choice territory or living range has been taken up or occupied, birds unfortunate in finding good range are likely to be forced into poor quality habitat, submarginal for the species (Chapters 11 and 12). Little study has been made of *ill-situated* birds, except for a few game species. But studies indicate that such birds live a rather more strained kind of life than well-situated ones. Birds banded in some environments have been reported to outweigh some in other environments, which indicates a probable relationship, difficult to evaluate though it may be. Bob-whites on poor range are more likely to lose weight (a fairly good indicator of body health) and numbers in severe winters than are those on good range. The loss of birds from unseasonable storm, as has been reported innumerable times both in the winter range and during migration, testifies further to drain upon the bird and its energy resources. Birds in smokey cities have been noted to have soot in the air passages, just as do many human beings. Those in areas of dust storms presumably would breathe in some dust. Ground birds are exposed to more blowing dust than an animal like man breathing air from somewhat higher above the ground.

PARASITES

Internal Parasites. Regular internal parasites of birds belong to five groups: Protozoa, Platyhelminthes, Nemathelminthes (Nematoda), Acanthocephala, and Arthropoda. The protozoan parasites of birds belong to the classes Mastigophora (Flagellates), Sarcodina (Amoeba), and Sporozoa (Herman, 1944). They occur mostly as blood and intestinal parasites, but some may be found in the muscle (e.g., *Sarcocystis*) and elsewhere in the body.

In a study of blood smears of eighty-one species of birds, about one-third showed blood parasites (Huff, 1939). A similar study on Cape Cod of 2,385 birds of sixty-one species showed blood parasites in 269 birds of twenty-seven species, the highest rate of infection being 60 per cent in the Chipping Sparrows (Herman, 1938). Blood smears of birds in general show varying amounts of infection from about 3 per cent to 100 per cent, depending upon the size of the sample and the time it was taken. Because in some diseases the acute stage when parasites can be detected easily in blood smears lasts but a short time, a higher incidence in birds than usually shown may be possible, perhaps as much as 50 per cent in marsh birds. Most of the protozoan blood parasites are malarial or are malaria-like in their action. Those commonly reported for birds are *Haemoproteus, Leucocytozoon*, and *Plasmodium*. Blood parasites spread to birds by means of insect intermediate hosts. Birds once infected by a malarial organism seem usually to be immune from reinfection by the same parasite. There are indications that the infection by a parasite may give some degree of immunity from other and especially closely allied malarias; in some cases, however, this is definitely not so.

Most protozoan intestinal parasites of birds belong to the order Coccidia. Two genera occur rather commonly in birds, *Isospora* and

Eimeria. A tendency has been noted for *Isospora* to be found in the taxonomically higher forms of birds and for *Eimeria* to infect the lower ones. These organisms cause the diseases known as *coccidiosis* by growing in the epithelial cells of the digestive tract, usually in the lining of the intestines. A high percentage of some birds (60 to 100 per cent of specimens in some studies) appears to be infected, but the balance between host and parasites seems such that birds show few ill effects. Yet one must assume, with considerable good reason, that a bird with them might suffer or be weakened by them when conditions for bodily vigor are poor. Birds with *acute* coccidiosis may show loss of appetite, emaciation, droopiness, and diarrhea, often followed by death. Birds become infected by picking up spores, usually with their food.

A number of flagellate parasites have been found in blood and intestines. Those in the blood are chiefly *Trypanosoma*; those of the digestive tract, usually in the intestines, are chiefly species of *Trichomonas.* The latter genus has been reported in small numbers and species from about half the orders of birds. *Trypanosoma* seems to be spread by arthropod intermediate hosts, *Trichomonas* by ingestion.

Cestodes (tapeworms) have been reported from many birds; they belong to several different genera. Indications point to a greater abundance in birds than mammals, possibly because cestodes of birds have a more marked *host specificity* than those of mammals. Several studies have indicated a greater incidence or menace of tapeworms to young birds than to adults. The incidence of parasitism by tapeworms has varied widely as reported in different investigations, from almost nothing to as high as 61 per cent. One young Blue Grouse is reported to have had ninety-three tapeworms that almost completely filled the intestines. Tapeworms need an intermediate host, and those of many common birds develop in insects from which the birds get them by feeding upon infected insects. Others develop in snails or crustaceans. *Diphyllobothrium oblongatum* develops in a fish that may be caught by a Gull and eaten by it or fed to its young, which would infect the adult or young.

Trematodes (flukes) are mostly internal parasites, though a few may form cysts in the skin. There are a large number of flukes parasitic upon birds, especially water birds. They may be found in the intestines, veins and ducts of the liver and pancreas, oviduct, bursa of Fabricius, caecums, trachea, kidney, and blood stream. Many of the flukes have as an intermediate host snails, crustaceans, aquatic insect larvae, fish, or tadpoles (Fig. 21·1). The cercarial stage of bird flukes (*Shistosoma*) may be one of the organisms involved in "swimmer's itch" (Worth, 1949b).

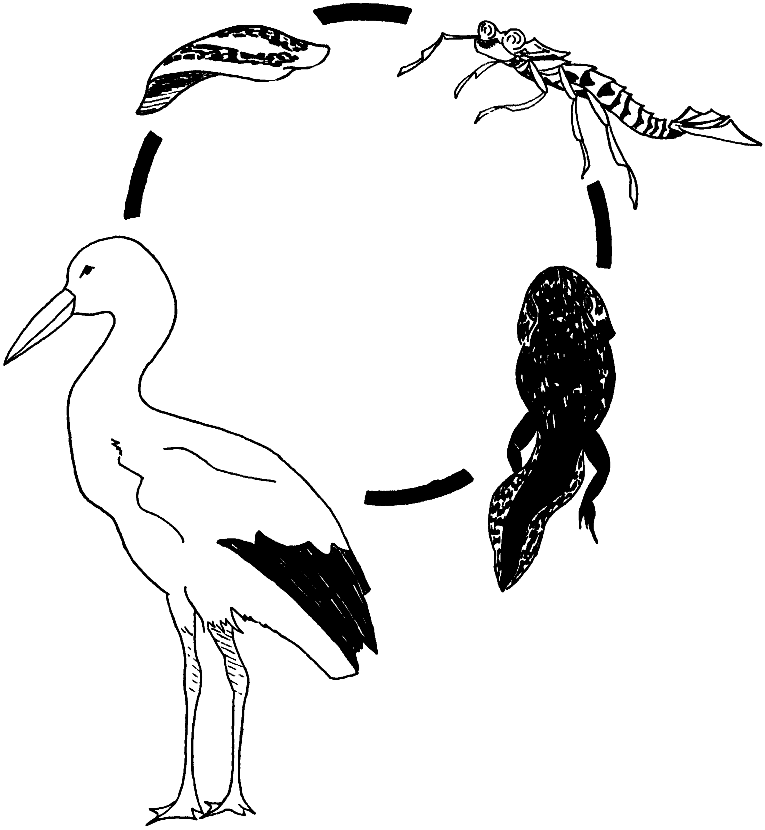

Fig. 21 • 1. *Life cycle of a trematode. Water birds infected with flukes may contaminate the water and in turn infect the dragonfly nymphs from which the chain passes to a tadpole eaten by a water bird, which becomes infected with flukes. (By permission from* Bird Life, *by Edward A. Armstrong, p. 139. Copyright, 1950, Oxford University Press, New York.)*

A very great number of nematodes (roundworms) have been reported from birds. They have been found in the proventriculus, gizzard, trachea, crop, intestines, caecums, eyes, and body cavity. Microfilaria have been found in the blood stream of a number of birds. Many nematodes have direct life cycles, and the birds become infected by feeding upon contaminated soil. Others require an intermediate host, such as a grasshopper, from which the birds get the parasites by eating infected insects. The caecal worm, *Heterakis gallinae*, carries the protozoan *Histomonas meleagridis* that causes the disease known as "blackhead."

Several spiny-headed worms (Acanthocephala) have been found in the intestines of birds. The intermediate hosts are crustaceans and insects from which the birds get the parasites by feeding upon infected animals.

Parasitism by *Reighardia* has been found in Gulls and Terns. The parasites belong to Pentastomida, wormlike animals of uncertain systematic position but usually placed in the phylum Arthropoda.

External Parasites. External parasites of birds belong to the phyla Annelida and Arthropoda. The former contains several leeches (*Hirundinea*) reported from water birds. Almost all other external parasites belong to the Arthropoda.

Parasitic arthropods of birds are of two classes, Arachnoidea (Acarina: ticks and mites) and Insecta (Mallophaga: biting lice; Dipteria: mosquitoes, black flies, bottle flies, hippoboscid flies; Siphonaptera: fleas). It is said to be possible for every kind of bird to have at least three kinds of lice, one or two hippoboscids, and several mites. Those feeding or alighting upon the ground may carry one or more kinds of ticks (Peters, 1936). In 239 species of eastern birds, ectoparasites were reported as follows (which may indicate relative distribution): lice 220, mites 61, hippoboscid flies 56, and ticks, 55.

Ticks and mites are external parasites living in the feathers or burrowing into the foot scales of birds or attaching temporarily for engorging on the blood of the host. During the season when ticks are most active, ground birds and those living in thickets may become heavily parasitized with ticks. Ruffed Grouse have sometimes been reported with head and neck literally covered with ticks. A red-eyed Towhee has been found with twenty-nine ticks attached to the head. In the winter grounds of the southern states, 10 to 20 per cent of ground birds caught in banding traps may carry ticks.

Fleas have been reported from birds, but little is known as to their harmfulness or role in transmission of disease.

Mallophaga as a rule live at the base of feathers. Some live off the feather parts and others from skin particles. A few feed upon the blood of the host and even upon the fluids of the eyes. Eggs are usually laid among the feathers. *Piagetiella* live among the feathers of Cormorants and Pelicans and even in the mouth, where they suck blood. They have specially adapted tracheas for their life in aquatic surroundings. Parasites are highly host specific, and parasite groups have large numbers of species. There are about 2,100 known species of Mallophaga, for example, which would suggest a total of 10,000 for all species of birds (Eichler, 1946).

Mosquitoes parasitize birds and the culicine mosquitoes transmit avian malaria (*Plasmodium*). Blackflies have been found to transmit *Leucocytozoon* malaria; hippoboscid flies transmit *Haemoproteus*. Mosquitoes (perhaps blackflies also) carry fowl pox. Hippoboscid flies, unlike mosquitoes and blackflies, spend their whole life cycle on birds or in the debris of nests. They are blood-sucking insects but are not known to cause ill health. Ticks may transmit tularemia to birds.

Nest Parasites. Studies of nests of birds have shown a surprisingly large fauna of insects and other animals, mostly harmless. But some nest parasites may be serious enemies of the nestlings. As many as a billion mites have been estimated for a nest box; such mites can be destroyed by creosote or kerosene.

The common nest parasites are maggots of flies (*Apaulina*, *Calliphora*, *Protocalliphora*) belonging to the fly family (Musidae) though sometimes listed as a family of their own, Calliphoridae. The fly lays eggs in nests of birds, and those of the Tree Swallow and Eastern Bluebird have been reported as particularly likely to be parasitized. Any nest, however, especially those in cavities and nest boxes, may be parasitized. Nests of sticks, like those of the House Wren, seem less desirable as an abode for parasites than those of Swallows. The larvae attack the nestlings, usually about the legs and feet, mostly at night, and retreat into the nest material in the daytime. In a study in New England, 94 per cent of the Bluebird and 82 per cent of the Tree Swallow nests were parasitized (Mason, 1944). In inclement weather when little food may be brought to the young, the attacks of the parasites upon weakened nestlings may cause death. More than 400 of the parasites were found in the nest of a Tree Swallow, but the more usual number when present seems to be from five to about sixty.

Host and Parasite Adjustment. Normal parasites and their hosts have evolved together and seem well adapted to each other. Closely related parasites evidence close relationship of their respective hosts (*Fahrenholz Rule*). If two groups of birds have three genera of Mallophaga in common, their close relationship is deemed established (Hopkins, 1942). Thus the Mallophaga of the Ducks, Geese, and Swans suggest that Geese and Swans form a distinct group, the Ducks another. Those of the Hummingbirds suggest a closer relationship to the Passerine birds than to the Swifts. The Herons and Storks may be more distantly related than assumed; parasites suggest that the Herons arose in South America and the Storks in Africa.

Predators often obtain temporary infections of parasites from their prey. In some cases, predators have appeared heavily parasitized, as though they served to concentrate the parasites of their prey. Flying ectoparasites like the hippoboscid flies would seem to have little difficulty in transferring from one bird to another, though they seem to spend most of their time deep in the feather coat. Flightless ectoparasites have several ways of transmission open to them. They may pass during direct contact, as between parents and nestlings or between birds in roosting flocks. Parasites attached to objects, such as branches, loose feathers, or nest material, may pass to another bird touching the objects. Some may transfer during free-living stages or by direct attachment such as of ticks and mites. Smaller parasites attached to a hippoboscid fly or other larger parasite could be transferred with the temporary carrier. Ectoparasites of prey species can be transferred to a predator or its young during feeding.

VIRUSES, BACTERIA, AND FUNGI

Virus Diseases. Probably the best-known virus disease of birds is *psittacosis* (page 407) because it on occasion may be transmitted to man (first known case in Switzerland, 1879). Seldom is it transmitted from one human to another. It has been reported from Parrots, Domestic Chickens, and Domestic Pigeons. A closely related virus has been reported from the Atlantic Fulmar.

Flies have been shown to carry the virus for *ulcerative enteritis*, and birds may become infected by eating infected flies. But it is more often spread by fecal contamination. Cases have been reported of a few birds (Pheasants, Pigeons, House Sparrows, Storks, and others likely to be found about farm yards) becoming infected with the virus responsible for sleeping sickness of horses (equine encephalitis). It has been found in newly hatched domestic chicks, which indicates that it can be egg-borne.

An avian cancer-like condition suggesting a filterable virus as the responsible organism and presumably transmitted by biting flies has been suggested as a disease found in a British Columbia Blue Grouse.

Bacterial Disease. The best-known bacterial disease of birds is the botulism sometimes called "western duck sickness." It has occurred a number of times in western water areas where conditions may be favorable at times. The causative organism has been determined as *Clostridium botulinus*, Type C. It develops in decaying organic matter in warm, moderately alkaline waters. For this reason, it seldom occurs in forested areas, where the waters are usually acid. Birds become sick by drinking water containing toxins produced by the bacteria. If taken in dilute amounts, a sick bird usually recovers, but continued or concentrated ingestion usually proves fatal. Great losses of Waterfowl and other birds have occurred in western waters (Kalmbach, 1934).

Birds feeding upon decayed meat, or upon maggots that have fed upon it, have become infected with a form of botulism. The body fluids of Vultures, however, seem to have antibiotic factors of unknown nature, so that they are resistant to disease organisms, toxins, and ptomaines harmful to most other birds or other animals. Bacteria (*Pasturella*), thought to be transmitted by mites, cause bird cholera. Ruffed Grouse and some other birds have had tularemia (caused by *Pasturella tularensis*). Avian tuberculosis has been found frequent among birds in contact with poultry, such as the House Sparrow, or among those eating refuse, such as the Gulls. A related bacterial disease has been reported as "pseudotuberculosis." Bird pneumonia also occurs.

Fungus Diseases. How widespread fungus diseases may be in wild birds is unknown, and the chances are that they are not common. Fungus diseases have been found often among zoo birds and sometimes among poultry. Possibly some of the avian tuberculosis or pneumonia-like diseases have been caused by fungi. *Aspergillosus* has been found pathogenic in a number of birds, such as Gulls, Ducks, Geese, Hawks, and Owls. Though usually found in the lungs, it has been reported also in the esophagus, viscera, and body cavity.

Birds, especially the Vultures, have been accused of spreading anthrax in domestic livestock areas, but there is no reliable evidence to indicate this. (There is also no evidence to indicate that birds may spread hog cholera or hoof and mouth disease.)

BIRDS AS DISEASE RESERVOIRS

Because birds have a high body temperature, few of the diseases of man attack them. Just as a high fever may destroy invading organisms in man, the fever-high temperature of birds seems to protect them. Conversely, few avian diseases attack man. An exception is the disease commonly called "Parrot fever" but known to medical science as *psittacosis.* (But because Pigeons in city parks may carry it also, it sometimes goes by the name of *ornithocosis.*) Prohibition upon importations of Parrots into the United States stems from the dangers of psittacosis, a highly fatal disease.

No wild bird of the United States and Canada is known to serve as the reservoir of any human disease. Birds have malarias of their own (some fifteen kinds) but none attacks humans. Yet because of bird malaria, birds (Canary, Chicken, Duck, Pigeon) have been used in testing new malarial control drugs (e.g., atabrine, plasmochin, paludrine, pentaquin, chloroquin) before trying them on human beings. Birds have also been used to study the life cycles of malarial parasites, particularly their "exoerythrocytic" stages.

A number of cases of birds becoming infected with diseases of domestic animals, particularly poultry diseases, have been recorded. But the chances of a human being getting a disease from any wild bird are practically nil. The chances of domestic stock becoming infected from wild birds are just about as low.

OTHER HEALTH FACTORS

Poisons. Birds have been found sick from a number of poisons besides insecticides (page 445). From time to time, American Robins and Cedar Waxwings feeding upon fermented fruit have been influenced by the alcohol of fermentation, showing all the signs of intoxication. "Intoxicated Robins" sometimes become the basis for newspaper stories and pictures.

Various alkalis in the water of dry regions if in sufficient concentration can cause severe irritation of the intestinal tract. Alkali poisoning, however, has been confused with both lead poisoning and botulism, so that it is not clearly understood.

Among some Waterfowl, the most serious single source of injury to birds outside of hunting itself is the danger of lead poisoning. Lead shot sinks to the bottom of lakes, streams, and marshes, where it is picked up by the feeding birds. The shots remain in the gizzard (because of gravity), where they may be ground up to be absorbed. Because lead is a cumulative poison, the number of shots in the gizzard may be few and yet the bird may be affected. From one to six No. 6 lead shot have proved fatal. There is no known treatment (aside from feeding and watering in pens and from "stomach cleaning"). Nearly all Waterfowl hunting areas are to Waterfowl a source of danger from lead poisoning. Many tons of shot have been fired over small areas. Such lead shot in water tributary to domestic water supplies is a source of contamination and of concern to health authorities as a menace to public health.

Birds have been poisoned by feeding upon insects killed by insecticides. They have been poisoned on many occasions in the course of widespread poison campaigns for rodent and predator destruction. Some studies have shown that insecticide sprays in low concentrations may control insect outbreaks without killing off the bird life. But of the effects from newer insecticides, little is known (page 446).

Injuries. Injuries of various kinds occur among birds. The one-legged Sandpipers occasionally seen along shores, for example, perhaps lost the other foot in an accidental encounter with a clam or other aquatic organism. Many accidents can happen to cause the loss or crippling of the feet in birds. One-legged Robins and other birds of the garden have been reported many times.

Birds have a remarkable ability to dodge twigs and other projections, but sometimes they fail to do so in flight and injury may result. A number of Ruffed Grouse have been reported with pieces of broken sticks completely imbedded in the body, yet the bird recovered. Head injuries usually result in death, probably always if the skull is fractured. Ptarmigan of the Arctic tundra are reported to be killed frequently by flying into telegraph wires, sometimes being completely decapitated. But the largest number of injuries probably occurs along highways as the result of collision with automobiles, some highways being littered with dead birds. This is especially true during the nesting season. Injuries at lighthouses have long been reported. Fractured bones may heal within a few days if the bird or bone remains motionless. Even wing bones have healed sufficiently after fractures to become usable again, though most broken-winged birds are doomed (Wood, 1941). Most birds recovering from wing fractures have had only the radius or ulna broken, so that the second member of the pair prevented displacement by muscle tension.

Freezing of the feet and other parts of the body ordinarily seldom happens, though the soft toes of Mourning Doves seem especially likely to become frozen in severe weather.

The injurious effect of oil pollution has brought disaster to birds on a number of occasions, both inland and along oceans. Oil mats the feathers and afflicted birds become water-soaked or chilled rather quickly. Oils may have a toxic effect also. Keeping oil from getting into the water is the only known means of preventing oil pollution and consequent injury to water birds from it.

Bathing. Many ground birds, like the Domestic Chicken or the Vesper Sparrow, maintain cleanliness by bathing in the dust. It may help control ectoparasites. Perhaps it aids health and general body comfort. While there is some chance of infection from contaminated soil, the advantages of cleanliness outweigh it. In dry soil exposed to the sun, especially in arid regions where dust bathing is most common, soil-borne infections seem few, probably because of the sterilizing effects of full and sustained sunlight.

Many birds use water for bathing, such as the American Robin, American Goldfinch, and Tufted Titmouse. Water birds, Shorebirds, and Passerine birds, as a rule, bathe in water (if they bathe at all). But exceptions occur as in the Vesper Sparrow that uses dust or in many birds of the arid regions. The House Sparrow, for example, has been observed to bathe in water as well as in dust.

SUGGESTED READING

BEISTER, H. E., and L. H. SCHWARTZ (eds.), *Diseases of Poultry*. Ames, Iowa: Iowa State College Press, 1948.

BOYD, ELIZABETH M., "The External Parasites of Birds: A Review," *Wilson Bulletin*, 63(1951):363–369.

CHANDLER, A. C., *Introduction to Parasitology*. New York: John Wiley & Sons, Inc., 1949.

HERMS, W. B., *Medical Entomology*. New York: The Macmillan Co., 1950.

HYMAN, LIBBIE HENRIETTA, *The Invertebrates*, 3 vols. New York: McGraw-Hill Book Co., Inc., 1951.

*ROTHSCHILD, MERIAM, and THERESA CLAY, *Fleas, Flukes, and Cuckoos*. London: Collins, 1950.

*STORER, TRACY I., *General Zoology*. New York: McGraw-Hill Book Co., Inc., 1951.

22

Rise of Bird Protection

For a long time in his history man killed birds, if he killed them at all, just as did the wild predator: when he chose, when he could, and as he pleased. But always he killed within the limits set by the crudity of his weapons—bare hands, clubs, snares, arrows—which alone guaranteed protection to birds except for nesting colonies that he might raid unaided by weapons. Just as the wild predator is unable to make its prey extinct in their respective native ranges, primitive man seemingly was not able to do so either (except possibly for Maoris preying upon the Moas).

HISTORICAL DEVELOPMENT

Early Bird Protection. The large and colorful birds no doubt first attracted man's interest (Figs. 22·1, 22·2) for food or for feathers, and in a sense they consequently received his first protection. Restrictions of a protective nature may well have been class distinctions, others perhaps religious taboos (Leopold, 1933). Because only one who had earned a *coup* might wear the emblematic Eagle feather, by that token, the Eagle received a measure of "protection" from the Indian. Birds sought, like the Quetzal, for adornment of a chieftain's costume only, received more "protection" from primitive hunters than those sought by all Indians. But we can rightly hold that the bird not sought at all was the best protected.

In early historic times, Kublai Khan protected "large birds" from March to October; Henry VII of England prohibited Herons from being taken except by Hawk or longbow; and James I decreed that "hail shot in hand guns" might not be discharged within 600 paces of a Heronry (Leopold, 1933). Henry VIII protected Waterfowl during the breeding season and James I added Pheasants and Part-

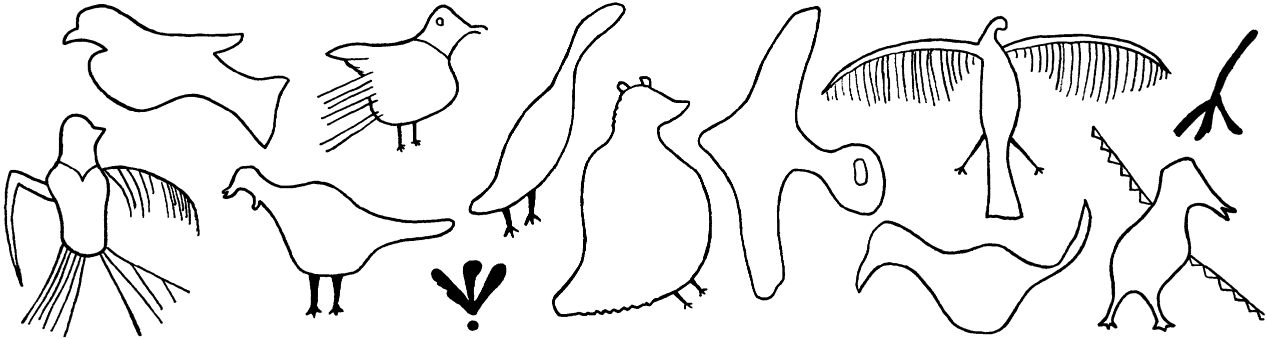

Fig. 22·1. *Picture writing of Texas Indians indicates that birds appealed to primitive man.* (*After A. T. Jackson,* Picture-Writing of Texas Indians. *University of Texas, Anthropological Papers, No. 3809, 1938.*)

ridges. But Henry VIII also put bounties on Crows, Choughs, and Rooks, which bounties Elizabeth I extended to the Magpie, Cormorant, Kite, and many other birds.

Until the coming of the shotgun and rifle, little universal protection was needed save for control against egging, hawking, nesting, snaring, or nest destruction. With the coming of gunpowder came the destruction of birds on a large scale and consequently greater need for protection. In addition, there arose the attitude that birds which made good targets took something of value from the hunter or the farmer. Even today, the uninformed or willful finds this reason enough for the destruction of birds and other wildlife by shooting, trapping, poisoning, and other means.

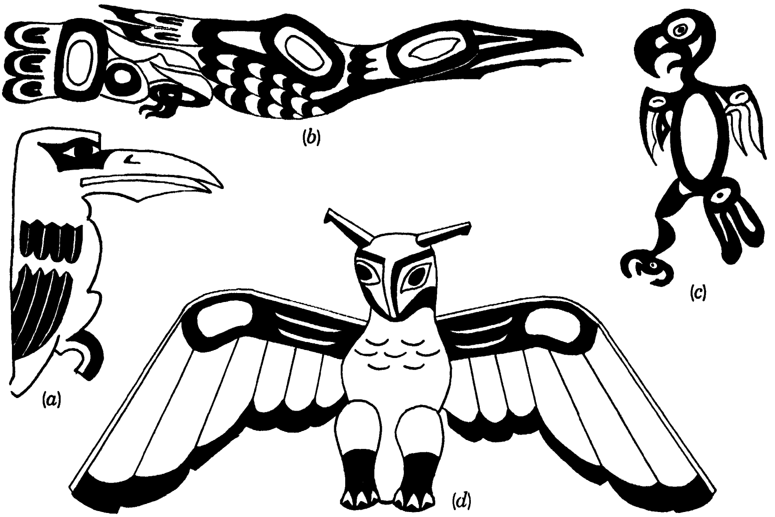

Fig. 22·2. *Bird designs in totem art of British Columbia Indians would seem to testify to an esthetic response to bird life. (a) Raven, (b) Red-shafted Flicker, (c) Eagle, and (d) Thunder-bird. (a, b, c after Alice Ravenhill,* An Outline of Arts and Crafts of the Indian Tribes of British Columbia. *Occasional Papers of the British Columbia Provincial Museum, No. 5, 1944; d from a totem pole.)*

Later Bird Protection. In England, the first *blanket protection* of songbirds, as distinguished from game birds, hunted birds, or predatory birds, seems not to have been legislated until a Parliamentary enactment of 1831 (Leopold, 1933). In the New World, the first regulation for game was enacted by the New Netherlands colony in 1629. The first songbird protection was that enacted by Massachusetts in 1818 which prohibited killing Robins between March 1 and July 4. The first blanket protection for songbirds appears in 1851 (Connecticut, New Jersey), and we may presume that little was needed or considered necessary before that time. By 1883, nineteen of the thirty-nine states had laws protecting nongame birds. All states of the United States and all provinces of Canada have since enacted blanket laws protecting songbirds, using the "Audubon model law" as the basis for legislation.

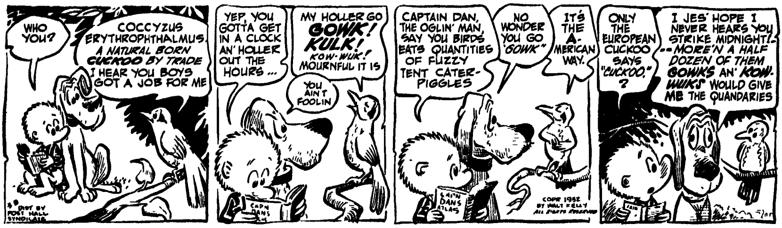
WHO YOU?
COCCYZUS ERYTHROPHTHALMUS. A NATURAL BORN CUCKOO BY TRADE I HEAR YOU BOYS GOT A JOB FOR ME
DIST BY POST HALL SYNDICATE
YEP, YOU GOTTA GET IN A CLOCK AN' HOLLER OUT THE HOURS ...
MY HOLLER GO GOWK! KULK! KOW-WUK! MOURNFUL IT IS
YOU AIN'T FOOLIN
CAP'N DANS ATLAS
CAPTAIN DAN, THE OGLIN' MAN, SAY YOU BIRDS EATS QUANTITIES OF FUZZY TENT CATER-PIGGLES
NO WONDER YOU GO 'GOWK'"
IT'S THE A-MERICAN WAY.
COPR 1952 BY WALT KELLY ALL RIGHTS RESERVED
ONLY THE EUROPEAN CUCKOO SAYS "CUCKOO." ?
I JES' HOPE I NEVER HEARS YOU STRIKE MIDNIGHT! -- MORE'N A HALF DOZEN OF THEM GOWKS AN' KOW-WUKS WOULD GIVE ME THE QUANDARIES

Fig. 22·3. *That the difference in voice between the American and European Cuckoos formed the basis for cartoon art speaks highly of interest in birds for their own sake. (By permission from the cartoon strip* Pogo, *by Walt Kelly. Copyright, 1952, Walt Kelly, Post-Hall Syndicate, Inc., New York.)*

In the nineteenth century, protection of nongame birds arose in part as a desire to protect them for themselves and in part to protect them as protectors of crops. In the early part of the twentieth century, protection became so universal in most of the English-speaking lands that songbirds are now protected almost wholly for themselves. Thus protection has become a *tradition*, the strongest form of control yet devised in a democratic society, and the importance of which is being continually indicated (Fig. 22·3).

Protection of Larger Birds. Protection of the larger and more spectacular birds, past and present, has lagged far behind that of songbirds. This is especially true of Hawks, Owls, and other birds alleged by some to be harmful. The fundamental motive, the desire to shoot something, still dominates treatment of predators and most large birds. When that motive is taken away, the willingness and zeal hunters and others use in killing predators should largely disappear and protection should be substantially as good as it was before gunpowder was invented.

The Kite, at one time perhaps the most familiar predatory bird in England, long ago became one of the rarest (Newton, 1893–1896).

The birds commonly rode the air currents over the city of London, from which habit came the term *kite* as applied to a child's toy in the air. Other Hawks and Owls have likewise declined in numbers and become scarce. In America, the larger birds have declined in much the same way, particularly so with the marked increase of hunters in the twentieth century and with the use of breech-loading shotguns in place of the old muzzle loader. As late as 1900, when there were fewer hunters (and more game), the number of Hawks clearly was still relatively high. Egg collecting as a hobby still had many advocates who seemed quite able to find Hawk nests in numbers in a day of search with horse and buggy.

The claim that blanket killing of predators will increase game has been demonstrated to be false. But many states and provinces still make exceptions in the nongame bird laws to remove protection from Hawks and Owls or from some, such as the Horned Owl, Cooper Hawk, and Goshawk. Because few hunters know one game bird from another, let alone the unprotected Hawks and Owls, all large birds are shot. To grant protection and to plug the loophole by which so many birds are destroyed, laws need readjustment. A model Hawk and Owl law providing that a *landowner* may kill one in the act of destroying his property has proved good. This protects the birds and the landowners (when need be) but removes the opportunity for hunters to make a game of shooting predators.

Ownership of Birds. The ancient and legal designation of wild animals, *ferae naturae*, means literally "animals of nature." Others are domestic animals. In the United States and Canada, animals *ferae naturae*, like other things of an ownerless nature (so far as they are capable of being owned), belong to the people. Because the state or province is the medium through which the people exercise the collective ownership, it is commonly said that the birds belong to the state or to the province.* In other countries, the custom may be different. A common one is for game birds to belong to the landowner and nongame birds to belong to the state.

Migratory Bird Treaties. The United States and Canada entered into a treaty, proclaimed December 8, 1916, for protection of birds that migrate between the United States and Canada. A similar treaty with the United Mexican States was proclaimed March 15, 1937. These two treaties mark an important event in the history of dealings between nations, for they dealt primarily with the protection of birds that the respective people might enjoy them.

* A discussion of this and related subjects of state, provincial, and federal controls in the United States and Canada will be found in Wing (1951).

Because songbirds already were well protected against hunters by their traditional status as nongame birds, the treaties served chiefly to curb hunters in some of their excess shooting of migratory game birds and many larger nongame ones. The inclusion of song and insectivorous birds made the coverage comprehensive and particularly served to bring the very great power of the bird-lovers and farmers to the aid of game protection. This fact is clearly shown in the language of the treaty and also in the United States Supreme Court decision * sustaining the original Migratory Bird Treaty which gave the treaty effect. †

Interest in Nature. Interest in nature as a form of enjoyment is a characteristic of the British, Teutonic, and Scandinavian cultures. It is less apparent among Latin, Slavic, Oriental, and other cultures. The underlying motives for this would surely be a fruitful source of philosophical inquiry. Since the whole subject of bird study is largely one of interest in birds because participants like birds and the outdoors, a long discussion of it seems unnecessary here.

Many organizations for bird protection and bird study have flourished from time to time. Many have been in operation for a great many years. The number of local and regional bird clubs in the United States and Canada probably exceeds a thousand. The leading four and their dates of organization are:

American Ornithologists' Union, 1883
Wilson Ornithological Society, 1888
Cooper Ornithological Society, 1893
National Audubon Society, 1901–1902.

Use of Bird Plumage. Nothing portrays so completely the militant spirit of bird protection as the battle of bird lovers with the millinery industry over use of feathers and sometimes dead bodies of birds on women's hats. ‡

Because America was a major disposal point for the booty of plume hunters, state laws and especially the Tariff Act of 1913 prohibiting importation, sale, and shipment of wild bird feathers largely ended the trade. It is reported that within 10 days after President Woodrow Wilson signed the 1913 Tariff Act, the London market declined (Henderson, 1927). It seems difficult to comprehend the quantities of birds killed. Between 1900 and 1908, twenty to thirty camps in Oregon were killing Grebes for feathers. In Venezuela, 1,500,000 Egrets were killed for plumes in 1898, and 400,000 Hummingbird skins were shipped to a single London dealer from the West Indies in one year. One London sale auctioned off 400,000 bird skins from America along with 350,000 from India.

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* Missouri *v.* Holland, 252 U. S. 416. It should be noted, however, that the correctness of this decision has been seriously questioned on the grounds that it establishes an unconstitutional principle that a treaty made under the Constitution may be invoked as authority for federal action not sanctioned by the Constitution itself. In other words, "a treaty for which the Constitution is the authority overrides the Constitution itself."

† 40 Stat. 755 (1918); 48 Stat. 1555 (1936).

‡ Magazines active in the campaign (e.g., *Bird-Lore*, *Ladies Home Journal*, *Saturday Evening Post*, etc.) contain many pictures of the plumage trade and stories of the bird lovers' battle. Files of these magazines can be consulted in most larger libraries.

That vigilance must be constant is shown in the raid of Japanese poachers to the Laysan Island bird sanctuary in 1909; they killed more than 200,000 birds, mostly Albatrosses (Dill and Bryan, 1912). More than 300,000 had been killed on Lisiansky Island (in 1905) before the slaughter ended. The need for vigilance in another direction was shown in the late 1930's. The Tariff Act of 1913 permitted the sale of feathers imported *prior to its passage.* A clause inserted in 1922 permitted importation of feathers accompanied by an affidavit that they were for the manufacture of fish flies. Through these two loopholes, unscrupulous importers poured thousands upon thousands of feathers during a revitalized style of wearing feathers (Pough, 1940). No feather of any wild bird has any appeal to trout or other fish over those of the barnyard Chicken; any assumed lure exists in the imagination of the fisherman.* Probably artificial flies made from some of the spectacular synthetic fibers and fabrics would do just as well and perhaps better.

Protection of Bird Colonies and Island Bird Life. Islands in the seas, especially remote from land, often develop curious and interesting bird faunas. Extraordinary tameness in dealing with man often characterizes island birds and must be credited to a long history, perhaps many millions of years, without contact with ground mammals (Fig. 22·4). The Terns of South Trinidad in 1913 alighted on the heads to peer into the faces of men in whaleboats. Albatrosses, the famed Gooney birds, seem not afraid of anything, not even the great caterpillar tractors, autos, or people on Midway Island. Hawks on Galapagos Islands allowed themselves to be touched, and Flycatchers tried to pull hair from visitor's heads for nest material (Carson, 1950). Rats coming ashore from a wrecked steamer on Lord Howe Island near Australia in 1918 nearly exterminated the bird life. Rats cause about three-quarters of the Tern losses on Cape Cod (Austin, 1948). Many islands of the South Atlantic have suffered terrible catastrophes to their bird and plant life from the followers of man—rats, goats, and pigs (Murphy, 1936). The Hawaiian Islands are truly a polyglot of alien birds introduced earlier by a misguided society for acclimatization of birds and today by equally misunderstanding sugar and pineapple interests (Fisher, 1948). Birds from many parts of the world now are found where once throve a unique and wonderful avifauna.

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* "Wild Birds and Fly-fishing: Is America Big Enough for Both?" Circular 47, National Audubon Society.

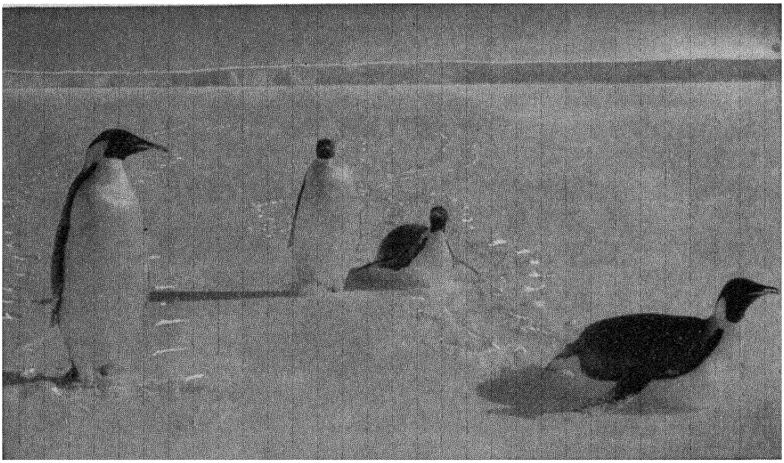

Fig. 22·4. *This group of Emperor Penguins tobogganing leisurely along on the snow changed their course and came up to the photographer for a curious inspection. It demonstrates the tameness of birds having little contact with man or predatory land animals. (Photographed at the mouth of the Bay of Whales by the U. S. Antarctic Expedition of 1939–1941. U. S. National Archives.)*

A complete list of the birds that have become extinct or extirpated on islands would be appalling. Many were destroyed by rats and pigs or man's destruction of the habitat. Many have been reduced by military installations, airplanes, airports, and dogs. Whether the rats on Midway or other islands could be exterminated is not clear, but it would be an easy matter for dogs (and cats) to be prohibited from being taken to such islands.

EXTINCT SPECIES

How many birds have become extinct since the Industrial Revolution is a question that cannot be answered with certainty. Sixty or more island forms have become extinct at the hands of man throughout the world; fewer have become extinct on continental land.

Nine forms of continental American birds have become extinct since the English settlements in America, with probable date of extinction as follows:

Great Auk	1853	Carolina Paraquet	1904
Pallas Cormorant	1852	Louisiana Paraquet	1904 (?)
Labrador Duck	1878	Eskimo Curlew	1930 (?)
Heath Hen	1932	Townsend Bunting	1832
Passenger Pigeon	1898 (1914)		

Great Auk. The Great Auk was a marine diving bird about the size of an ordinary barnyard Goose. It lived along the North Atlantic coasts where it nested along the shores of Norway, Orkney Islands, Faroes, Newfoundland, Labrador, Iceland, and Greenland. In winter it moved south to Maine and Massachusetts (occasionally farther) in the New World, and to Denmark, France, and northern Spain in the Old. The bird was unable to fly; its wings were merely flippers, from which it sometimes gained the name of "Penguin," a corruption of "pin-wing." Like most sea birds the Auks had a heavy layer of fat, which proved to be a source of oil and their undoing. For this oil and as food also, the birds were relentlessly pursued. How many birds the oil gatherers killed is not known, but at the height of the oil business, the numbers doubtless ran into scores of thousands of Auks a year. The birds were usually killed with clubs on land where they were helpless or clubbed in the water where they showed little fear of man. Concentrations of birds at the nesting grounds particularly drew the despoilers.

The last bird found on the great nesting ground of Funk Island appeared in 1840. One was reported for Iceland in 1844; the last living bird was seen in 1852, but a dead bird was picked up in Trinity Bay, Ireland, in 1853. Though people have written of the "unknown cause" of its extinction, killing by man is the correct one (Newton, 1893–1896). Only about eighty mounted and unmounted specimens, four skeletons, and a few eggs are known to be preserved. The American Ornithologists' Union publishes its quarterly journal under the title of *The Auk* in memory of the extinct Great Auk.

Pallas Cormorant. The Pallas Cormorant was discovered in the Bering Islands off Alaska in 1741 by the expedition of Vitus Bering. He reported them there in some abundance, but the bird became extinct by 1852. The exact sequence is unknown, but the birds were killed ruthlessly for food.

Labrador Duck. The breeding grounds of the Labrador Duck remain unknown, and the bird became extinct without its nest having been found. Probably it nested on the Ungava coast, the western part of Labrador. It wintered along the Atlantic Coast from Nova Scotia to New Jersey and perhaps to Chesapeake Bay, the heart of the market hunting and shooting country. The reason for its extinction is excessive shooting. The last authentic record of the Labrador Duck was December 12, 1878.

Heath Hen. From Maine to Virginia and perhaps west into Pennsylvania and Ohio lived an eastern form of the Prairie Chicken known as the Heath Hen. It obtained its name because the Pilgrims found it living rather abundantly upon the coastal areas and brush regions of the East, especially Cape Cod, Long Island, and similar areas of shore and scrub pine.

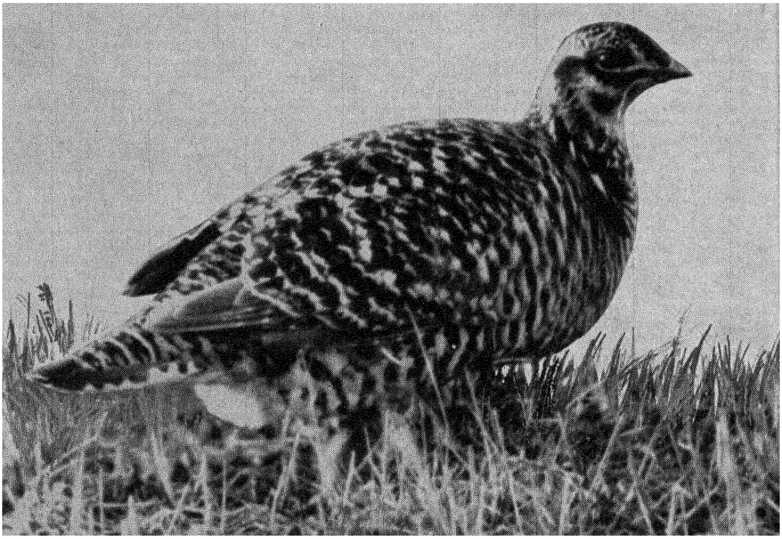

Fig. 22·5. *The last Heath Hen. Male photographed on Martha's Vineyard, Massachusetts, March 31, 1930. (Photograph by A. O. Gross.)*

By 1840 they were gone from the mainland of Massachusetts and Connecticut, though persisting longer on Long Island and the barrens of New Jersey and eastern Pennsylvania. By 1870 they had become restricted entirely to the small island of Martha's Vineyard off the southeast coast of Massachusetts. In 1890, there were some 200 birds on the island, but the number dwindled to about 100 in 1896 and to 50 in 1908, when a reservation was established for them. Intensive effort of Massachusetts people increased the number to about 2,000 in 1915, when they were well distributed over the island.

But an unfortunate sequence of events followed, which because uncontrolled spelled the doom of the birds. Fire swept the island on May 2, 1916, burning some twenty square miles of area and destroying many nests and birds. The following winter was exceptionally severe, so that in 1917, only 150 birds were found. Most are believed to have been males, which probably reflected the heavy loss of incubating females in the spring fire of 1916. In 1920, domestic Turkeys brought to the island apparently introduced blackhead and other diseases. By 1927, the number of Heath Hens declined to eleven males and two females. In the fall of 1928, only two males were found and on December 8 but one male remained. This bird persisted until last seen February 9, 1932 (Fig. 22·5).

Passenger Pigeon. Passenger Pigeons formerly nested from central Mackenzie, southeast to central Quebec, and Nova Scotia, south to Kansas, Mississippi, Kentucky, and Pennsylvania. They wintered from Arkansas and North Carolina south to Texas and Florida. The general range of the bird appears to have covered most of the area between the Rockies and the Atlantic.

The Passenger Pigeon migrated and nested in flocks so large as to seem almost unbelievable (page 256). They nested in great colonies, where each female laid but a single egg. People killed them at all seasons of the year, on their nesting grounds, in migration, and in winter. (A similar situation still exists in the White-winged Dove colonies of northern Mexico, where "sportsmen" stand at the roadsides and shoot great numbers of Doves returning to the nests in the late afternoon.)

The first law to protect the Pigeon seems to have been enacted by New York in 1867; Michigan gave a small measure of protection in 1869; Massachusetts in 1870, and Pennsylvania in 1878. The last bird reported in the wild was in 1898, when some were seen at Lake Winnipegosis, Manitoba, April 14; July 27 at Owensboro, Kentucky; September 14 at Canandaigua, New York; and September 14 at Detroit, Michigan. Despite real interest no authentic reports have occurred since, except for one fairly reliable report of birds at Babcock, Wisconsin, in September, 1899. The last known specimen died in the Cincinnati Zoo at the age of 22 years in 1914; it had been hatched in captivity. A monument commemorating the Passenger Pigeon has been erected in Wyalusing State Park, Wisconsin.

Contrary to popular belief, the Passenger Pigeon did not "disappear overnight," but its disappearance was a progressive one extending over a 50-year period or longer (Schorger, 1937). Because of its erratic habits, its absence in an area was attributed to a shift of flights rather than to a decline in numbers. Many causes and circumstances contributed to the extinction of the bird. Among them were the cutting of timber and settling of the land where they nested, the habit of laying but a single egg, nesting but once a year, destruction during nesting, and destruction in migration and in winter.

Paraquets. In southeastern and central United States formerly lived a species of Paraquet separated into two subspecies known respectively as Carolina and Louisiana Paraquets. (The latter, interestingly enough, was described as new to science only after extinction.) These birds formerly lived north from Florida to southern Virginia and west to Indiana, Oklahoma, and Louisiana. The only member of the Parrot family resident in eastern United States, the birds were reported in large flocks by observers in the early 1800's. The last one in Illinois was seen in 1861; none has been seen in Louisiana, Mississippi, Kentucky, or Tennessee since 1880. The last one disappeared from Kansas and Missouri in 1904. An obscure report placed them in Florida as late as 1914 and possibly 1920. The Paraquets became extinct because of destruction of their habitat and shooting the birds for food and as destroyers of crops. Their Parrot nature of returning and hovering over a fallen comrade made it possible for a gunner to destroy a whole flock.

Eskimo Curlew. The Eskimo Curlew formerly nested on the Barren Grounds and migrated in autumn southeastward to the coast region extending from Labrador to New Jersey. From there it crossed the western Atlantic to South America and wintered in the Pampas country. Audubon visited Labrador in 1823 and gives us this description of their numbers: "The accounts given of these birds border on the miraculous. They arrive in such numbers to remind me of the Passenger Pigeon." In spring they migrated northward through the continental interior. The great flocks were decimated at all seasons of the year (save possibly on some of the nesting grounds), from Labrador to Argentina and back through the interior of North America. By 1890 only a few scattered flocks were reported anywhere. The last individuals reported are about as follows: Ohio, 1878; Michigan, 1883; Indiana, 1890; Wisconsin, 1912; Argentina, 1925; and Nebraska, 1926. Unconfirmed but evidently reliable reports have placed Eskimo Curlews in Labrador as late as about 1930 and probably a few scattered elsewhere during the following years.

Townsend Bunting. The Townsend Bunting, a close relative of the Dickcissel, has puzzled taxonomists, who have been unable to ascribe its characters to hybridization. This leads to the suggestion that it may have been an ancient species that became extinct (1832) before a second specimen was obtained.

Island Birds. Birds reported extinct upon islands adjacent to North America are:

Black-capped Petrel	1920 (?)
Guadalupe Caracara	1900 (?)
Cuban Tri-colored Macaw	1864
Gosse Macaw	1800
Guadeloupe Macaw	?

The birds that appear to have become extinct on the islands of the world are numerous; yet we are unable to record with any certainty the extinct ones on the islands near North America.

The finding of a few living individuals of supposed extinct birds gives some hope from time to time that others considered extinct may still be found. The Cahow, a Bermuda Petrel supposed to have been extinct, has been found in very small numbers at Bermuda. A few individuals of *Notornis*, a flightless member of the Coot and Rail family have been found alive in some remote meadows of New Zealand after long having been considered extinct. But the possibilities of finding many supposedly extinct birds extant are greater than the probabilities.

When the Dutch discovered the island of Mauritius toward the end of the sixteenth century, they found a very large, flightless member of the Pigeon family, the Dodo. It was easily killed by men but especially by hogs gone wild. The bird was termed stupid because it had no fear of man, and the word *dodo* still means a stupid one. Another extinct Dodo lived on the island of Réunion to the south of Mauritius, where also lived a now-extinct Starling. On the island of Rodriguez, to the east of Mauritius, lived many interesting birds now extinct: a Dodo (called the Solitaire), Owl, Parrot, Dove, Heron, Rail, and a flightless Rail. Clearly, the protection of island bird life is probably the most important single need in international protection of birds. Continental forms with their large populations and large land areas have far fewer difficulties in surviving.

RARE AND THREATENED BIRDS

It would not be possible to list all the rare or threatened birds of the world, for rarity often means only that the region wherein the species is rare lies at the edge of the range. Within the United States and Canada, however, are a number of birds that should be considered as rare or threatened species:

Great White Heron
Glossy Ibis
Ross Goose
Spruce Grouse
Attwater Prairie Chicken
Sage Grouse

Trumpeter Swan
California Condor
White-tailed Kite
Swallow-tailed Kite
Mississippi Kite
Everglade Kite
Red-bellied Hawk
Short-tailed Hawk
Zone-tailed Hawk
Sennett White-tailed Hawk
Gray Hawk
Harris Hawk
Mexican Black Hawk
Audubon Caracara
Peregrine Falcon
Aplomado Falcon
Franklin Grouse
Masked Bob-white
Whooping Crane
Sandhill Crane
Roseate Tern
Aleutian Tern
White-crowned Pigeon
White-winged Dove
Red-billed Pigeon
Florida Burrowing Owl
Thick-billed Parrot
Ivory-billed Woodpecker *
Colima Warbler
Golden-cheeked Warbler
Kirtland Warbler
Sutton Warbler (probably a hybrid)
Cape Sable Seaside Sparrow

Efforts to Protect Rare and Threatened Species. While credit must go to the United States and Canada for their efforts to protect some of the rarer and threatened birds, the blame for the birds needing extra effort must go with the praise. The most promising development is not an official one at all but the simple recognition by many people (particularly those connected with "tourist industries") that the presence of a unique bird or other animal can be a source of civic pride and even attraction. Thus, guides along the Florida Keys point out the Great White Herons, Roseate Spoonbills, and other birds as attractions, which status their appearance and uniqueness rightly confer upon them. The establishing of a bird as a living symbol, such as that of the Bald Eagle as the American national emblem, gives it protection (except in Alaska). A special form of "living public monuments" has been proposed as a protective status, just as historical sites are protected as historical monuments.

Great White Heron. The Great White Heron, a pure white bird about the size of the Great Blue Heron, lives in the Florida Keys. It has never been an abundant bird in comparison with other Herons, and has been reduced in numbers by man's pre-empting its habitat, by malicious shooting (simply because it was a large and an easy target), and killing of young in the nests by fishermen. Some have been destroyed by hurricanes, especially important destructive agents when the birds are in low numbers. Prime credit for its protection should go to the National Audubon Society and also to the Florida Game Department. The establishment of a Federal Wildlife Refuge makes certain that still more protection will be afforded the species.

* Probably extinct.

Roseate Spoonbill. The Roseate Spoonbill formerly inhabited much of the Gulf coast region from Texas to southern Florida, southward to Argentina and Chile. The birds were forced out of the Gulf coast, largely by hunters, but are staging a comeback under increased protection (Allen, 1947).

Ross Goose. The Ross Goose is a small white goose about the size of a Mallard Duck. It breeds along the Perry River west of Hudson Bay in an area so small that its nest was unknown until 1938. There are probably fewer than 6,000 of the birds as a total population. The birds migrate south to winter in the Sacramento and San Joaquin valleys of California.

Trumpeter Swan. The original breeding range of the Trumpeter Swan extended from Alaska across to James Bay and south to Indiana, Missouri, Wyoming, and Montana. The birds have been reduced in number by shooting and settlement of the range. Remnant populations of the birds live in Yellowstone Park, Red Rock Lakes of Montana (near the Yellowstone), and in British Columbia. The increase in numbers has made it possible to transfer breeding stock to other areas.

California Condor. The California Condor lived along the Pacific Coast region from Lower California north to at least the lower Columbia River. By 1930, the birds had dwindled to a few in the Coast Range of southern California. Because the Condor was a large and clumsy bird, it fell easy victim to malicious shooting. Its habit of perching during early morning and cloudy weather made it an easy target. Many died from eating carcasses put out as poisoned bait by ranchers and the Biological Survey (more recently Fish and Wildlife Service), a greater danger to all birds now than ever before because poison campaigns are more widespread and efficient.

The birds lay but a single egg on bare ledges, and nest every other year, perhaps at longer intervals. Incubation takes a month and the young are covered with down in another 2 months. They become fully feathered at about 5 months and are able to fly somewhat later. Five years seem necessary to reach adulthood (Koford, 1953), when the birds weigh about 20 pounds and have a wing spread of 9 to 10 feet. They are a relatively ancient species, more widespread in the Pleistocene (see Fig. 9·5).

Attempts to protect the Condor from extinction have centered around protection from disturbance and especially people with guns. The Forest Service has closed the remnant area to people. But the supposed presence of extractable natural resources has caused pressure for commercial entrance to the area, which probably would spell the doom of the species. Continuance of poison campaigns likewise is a danger that the Condor may not be able to overcome.

Kites. The Kites all are gentle birds, never destructive of any real or assumed interest of man. The White-tailed Kite formerly ranged from California to Florida and south to Lower California and Guatemala. It has never been abundant in the United States, and probably is found now in but a few California locations. The Swallow-tailed Kite formerly ranged as far north as Minnesota, but is found now only along the Gulf coast area. The Mississippi Kite formerly inhabited the region from southern Illinois and South Carolina south to Florida and Texas. It is found today only in the Mississippi Valley and adjacent country.

The Everglade Kite ranged formerly from northern Florida south to South America. Fire and drainage in the Everglades have reduced the number of birds, along with the ever-present shooting and disturbing of large birds by people everywhere.

Unique among Hawks and Falcons—in fact, unique among birds—is its method of feeding upon snails of the genus *Ampullarius*.* The Kite darts and skims about over the pools and their shores, usually during late afternoon when snails move about most and crawl from the water onto the stems of vegetation. It grasps a snail in one foot and retires to a perch, still holding the snail gently in one foot. The bird makes no attempt to obtain its food by force; it waits for the voluntary extension of the animal from the shell. When this happens, the Kite quickly pierces the snail behind the operculum, always in the same place, which is evidently a nerve plexus. The Kite then sits and waits again, with the snail spiked on its bill, from which it stands out like a bump as large as the bird's head. Gradually the muscles of the numbed snail relax. After two minutes, more or less, the Kite vigorously shakes its head and swallows the mollusk, operculum and all, before the empty shell has reached the ground. The fragile shell never is broken or abraded by the captor. The long, slender bill, delicate and rather flexible, serves not as a hook but as a lancet or poniard. It is a case of instinctive correlation as exact as that of the spider-paralyzing wasps.

Audubon Caracara. The original range of the Caracara extended from Arizona to Florida and south to South America. The numbers of the bird have been reduced by shooting and disturbances of settlement. As the national emblem of Mexico, the Caracara frequently is called "Mexican Eagle."

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* Dr. Robert Cushman Murphy generously supplied the description of Kite feeding from his unparalleled opportunity for observation in the Argentine pampa.

Attwater Prairie Chicken. The original range of the Attwater Prairie Chicken was unique in that it was separated from the main range of the Prairie Chicken. It covered a rather small area on the Texas Gulf coast. The species has been greatly reduced in numbers by shooting, farming, and ranching. The increase of brush on many ranches as the result of overgrazing and destruction of grasses and forbes seem to have hurt the Chicken also. Little has been done to try to restore the birds, principally because people in the region are not sufficiently aware of its unique character, and official bodies have been concerned primarily with birds in numbers sufficiently large to interest hunters.

Whooping Crane. The Whooping Crane formerly bred in small numbers over the region from Hudson's Bay to the Mackenzie River south to about Nebraska. Today, the only remnant winters on the Gulf coast of Texas (chiefly in Aransas County) and breeds in northern Canada. The nesting place of the remnant or part of it was found in the summer of 1952 to be near Great Slave Lake. The Cranes migrate south across the plains country. They seem to stop in the Platte River Valley in Nebraska. Some birds are shot each year by hunters. Because the birds number fewer than a score (page 261), any shooting is a disaster to the species. The Aransas National Wildlife Refuge has been established for the Cranes, though in its actual administration, oil, cattle, and deer have a higher "priority" than the Cranes.

Ivory-billed Woodpecker. The Ivory-billed Woodpecker (possibly extinct) formerly inhabited the southern swamps from the Carolinas to Louisiana and East Texas, north to Oklahoma, Kentucky, and Missouri river bottoms. This Woodpecker, the largest of all American Woodpeckers, is reported to have a bill especially adapted for scaling bark from recently dead cypress trees to get borers underneath. Because its supply of food is so restricted, only mature trees furnished it in quantity. Hence, the species suffered from the lumbering of cypress timber.

ATTRACTING BIRDS

Winter Feeding. Few things testify so frequently to the compassion of man toward birds as winter feeding. It should be borne in mind always that birds must find something to eat and must withstand the elements by their own efforts at all times. When a human looks out of the window from its safe side during a storm—winter, spring, fall, or summer—he should bear in mind the inescapable fact that birds must live in all types of weather. No matter how severe the storm or how bad the weather, a bird still must look for food. The length of time that it can "hole up" is limited.

Bird-feeding trays adorn many home grounds, along with bird boxes of summer. Insectivorous birds require animal foods, which customarily are fed to them as suet or chopped meat. Seed-eaters will eat little except small grains, cracked corn, and chopped nuts. But Nuthatches, Chickadees, and their companions will eat a variety of foods—seeds, grains, or suet. Birds that feed upon berries and fruits, like the American Robin, will eat raisins, apples, and other similar foods.

Foods commonly used in winter feeding and some examples of birds using them follow:

Suet: Woodpeckers, Jays, Chicadees, Nuthatches
Small grains: Jays, Thrashers, Mockingbirds, Cardinals, Finches, Juncos
Sunflower seeds: Chickadees, Nuthatches, Cardinals, Grosbeaks, Finches
Raisins: Mockingbirds, Thrushes, Waxwings
Apples: Waxwings, American Robins, Cardinals

Trays for feeding may be a window shelf, a tree shelf, a trolley shelf, or a feeding shelter (Fig. 22·6). Some birds may be fed by scattering grain upon the ground. Snow may cover scattered grain, and ground-feeding birds need some assurance of protection from dogs

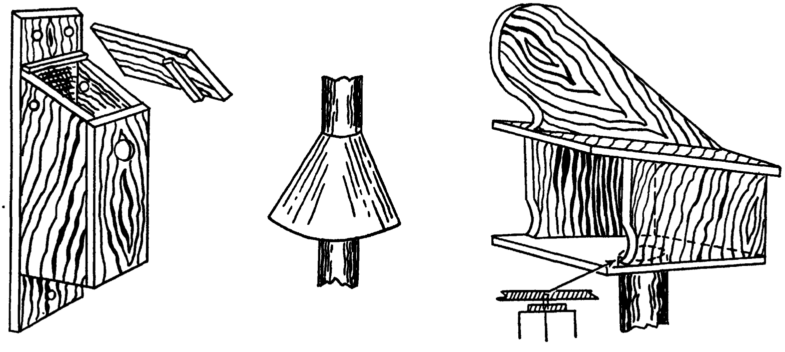

Fig. 22 • 6. *Many kinds of bird houses can be made, that on the left in mass production by use of six machine-cut pieces. The top may be lifted off for cleaning and disinfecting. Sometimes cats and squirrels must be kept from a feeding station, nest box, or tree; a guard such as that in the center may be effective. A revolving feeding shelter as shown at the right will prevent snow, rain, or wind from covering or blowing out the food. If House Sparrows are a nuisance, the front may be made into a hinged shelf held by rubber bands or weak springs. House Sparrows tend to avoid such a shelf, though native birds do not seem to mind it.*

and cats. Feeders often are placed on posts or platforms or covered by a brush shelter loose enough to protect an escaping bird.

Summer Feeding. Summer feeding differs little from winter feeding except that animal foods like suet are less sought after than in winter and are also more likely to spoil. In some gardens, more birds come to feeding stations in summer when adults seek food for young or when the young are about than at other seasons. Water attracts birds in hot weather especially but at other times of the year also and can be provided as a bird bath, fountain, or dish. In winter, a dish warmed by an electric light bulb below it will be kept from freezing. Some birds seem more attracted to water than others. In the North, Bohemian Waxwings come to water in winter possibly more than any other species. American Robins, Grackles, Song Sparrows, and Mockingbirds are regularly attracted in warm weather and sometimes in cold weather also.

Planting for Birds.* The shrubs and trees planted for bird foods vary throughout the continent, so that few general suggestions can be made. The leading shrub or tree fruits are mulberry, blackberry, rose, mountain ash, cherry, elderberry, service berry (*Amelanchier* spp.), sumac, holly (*Ilex* spp.), grape, dogwood, and *Viburnum.* In some areas, plants like thorns (*Crataegus* spp.), red cedar (*Juniperus*), oak (spp.), bayberry, and others are especially important, but a large number of native woody plants are usable (Van Dersal, 1938).

Small weed patches or food patches of grains are eagerly sought by many migrating and wintering birds. Small grains of several varieties can be planted, alone or in mixture. Among those used are corn, feterita, milo-maize, millet, soybean, buckwheat, sunflower, and others (Baker, 1941; Wing, 1951).

Provisions for Nesting Sites. For nesting sites, thick shrubs having numerous forks and branches are preferred by many common birds. Vines trailed over bushes and trees may be useful. A wide variety of trees and shrubs may be used, depending upon the region and site. Considerable success has been had by dwarfing, cutting, twisting, and tying branches for shelter.

Nest boxes have long been provided by man; even tribesmen in many parts of the world have put out hollow gourds for birds. Nest boxes may be of many sizes and shapes and of many materials. The more natural-looking they are perhaps the better, though how much preference birds show for various types of houses still remains a question. A convenient style that may be produced in mass is shown in Fig. 22·6. Boxes of wood and other material of low heat conductivity are preferable to metal ones, which may cause overheating. Most common birds tend to prefer houses in full or nearly full sun for part of the day at least. Some recommended dimensions are shown in Table 22·1.

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* The *Audubon Guide to Attracting Birds* (Baker, 1941) should be consulted for detailed information on attracting by planting, feeding, providing nest boxes, providing water, and providing sanctuary. *Practice of Wildlife Conservation* (Wing, 1951) has much information on planting and feeding along with other management practices for birds.

Table 22·1

Sizes of Nest Boxes and Recommended Height Above Ground

Species	Floor of Cavity (In.)	Depth of Cavity (In.)	Entrance above Floor (In.)	Diameter of Entrance (In.)	Height Above Ground (Ft.)
American Sparrow Falcon	8 x 8	12–15	9–12	3	10–30
Barn Owl	10 x 18	15–18	4	6	12–18
Saw-whet Owl	6 x 6	10–12	8–10	2½	12–20
Screech Owl	8 x 8	12–15	9–12	3	10–30
Hairy Woodpecker	6 x 6	12–15	9–12	1½	12–20
Downy Woodpecker	4 x 4	8–10	6–8	1¼	6–20
Red-headed Woodpecker	6 x 6	12–15	9–12	2	12–20
Golden-fronted Woodpecker	6 x 6	12–15	9–12	2	12–20
Flickers	7 x 7	16–18	14–18	2½	6–20
Crested Flycatcher	6 x 6	8–10	6–8	2	8–20
Phoebe	6 x 6	6	*	*	8–12
Violet-green Swallow	5 x 5	6–8	1–5	1½	10–15
Tree Swallow	5 x 5	6–8	1–5	1½	10–15
Barn Swallow	6 x 6	6	*	*	8–12
Purple Martin	6 x 6	6	1	2	15–20
Chickadees	4 x 4	8–10	6–8	1⅛	6–15
Titmouses	4 x 4	8–10	6–8	1¼	6–15
Nuthatches	4 x 4	8–10	6–8	1¼	12–20
House Wren	4 x 4	6–8	1–6	1	6–10
Bewick Wren	4 x 4	6–8	1–6	1	6–10
Carolina Wren	4 x 4	6–8	1–6	1⅛	6–10
Bluebirds	5 x 5	8	6	1½	5–10
American Robin	6 x 8	8	–	–	6–15
House Finch	6 x 6	6	4	2	8–12
Song Sparrow	6 x 6	6	†	†	1–3

* One or more sides open.
† All sides open.

Source: By permission from *Practice of Wildlife Conservation*, by Leonard W. Wing, p. 303. Copyright, 1951, John Wiley & Sons, Inc., New York.

Birds that nest on cliffs, ledges, and the like, sometimes take to man-made structures (Fig. 22·7). The Chimney Swift nests and roosts in chimneys, and at least one interested ornithologist built an artificial structure for them. Horizontal wooden strips nailed across the side of a barn under the eaves increased the number of Cliff Swallows on a Wisconsin barn (Buss, 1942). Additional aid seemed de-

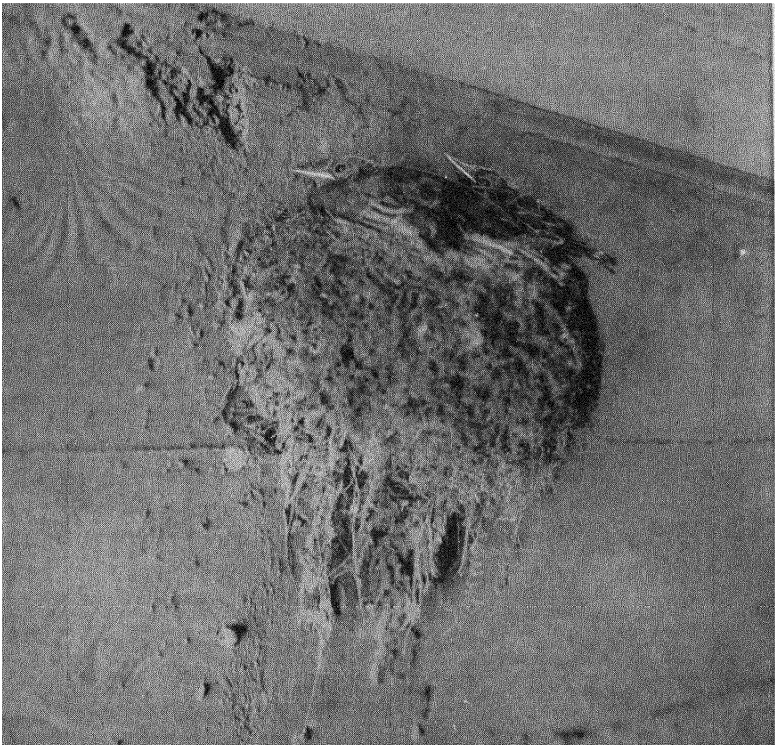

Fig. 22 • 7. *An uneven spot in the masonry of a culvert provides support for the Phoebe nest. Putting a slot in the form for the concrete would leave a usable ledge for the Phoebes; one in each new culvert would greatly increase the Phoebe population. (By permission from* Practice of Wildlife Conservation, *by Leonard W. Wing, p. 304. Copyright, 1951, John Wiley & Sons, Inc., New York.)*

sirable in the form of a mud source within three-quarters of a mile, House Sparrow control, and removal of old nests each fall.

Nesting material may be provided for some birds. Egrets have taken sticks, Gulls and Terns may use straw, and Eastern Goldfinches will take cotton. American Robins will carry off string or yarn, but the pieces should be not more than about a foot long to prevent tangling and subsequent tragedy. Chipping Sparrows have taken hair, and several birds have used moss provided for them. Providing mud to Robins, Swallows, and others that use it in the nest is obviously a help.

SUGGESTED READING

ALLEN, ROBERT PORTER, *The Roseate Spoonbill.* National Audubon Society, Research Report No. 2, 1942.

ALLEN, ROBERT PORTER, *The Whooping Crane.* National Audubon Society, Research Report No. 3, 1952.

*BAKER, JOHN H. (ed.), *The Audubon Guide to Attracting Birds.* Garden City, N. Y.: Doubleday & Co., Inc., 1941.

*BEARD, DAN (ed.), *Fading Trails.* New York: The Macmillan Co., 1942.

*GABRIELSON, IRA N., *Wildlife Conservation.* New York: The Macmillan Co., 1941.

HENDERSON, JUNIUS, *The Practical Value of Birds.* New York: The Macmillan Co., 1927.

HORNADAY, WILLIAM T., *Our Vanishing Wildlife.* New York: New York Zoological Society, 1913.

KOFORD, CARL B., *The California Condor.* National Audubon Society, Research Report No. 4, 1953.

PEARSON, T. GILBERT, "Fifty Years of Bird Protection," in *Fifty Years' Progress of American Ornithology, 1883-1933.* Lancaster, Pa.: American Ornithologists' Union, 1933.

PEARSON, T. GILBERT, *Adventures in Bird Protection.* New York: Appleton-Century-Crofts, Inc., 1937.

ROTHSCHILD, WALTER, *Extinct Birds.* London: Hutchenson & Co., 1897.

*SCHORGER, A. W., *The Passenger Pigeon: Its Natural History and Extinction.* Madison, Wis.: University of Wisconsin Press, 1955.

TANNER, JAMES T., *The Ivory-billed Woodpecker.* National Audubon Society, Research Report No. 1, 1942.

*WING, LEONARD W., *Practice of Wildlife Conservation.* New York: John Wiley & Sons, Inc., 1951.

23

Economic Relations of Birds

The economic values of birds to man may be listed for brevity as *positive*, *negative*, or *neutral*. No native American bird has negative values outweighing its positive ones. Even so persecuted a bird as the Crow, the Hawk, or the Owl has "beneficial" values greater than "harmful" ones, though hunters who find less game year by year like to believe otherwise. Birds do "favors" for man season in and season out; any "harmful" acts are of short duration, but man remembers them long.

Most of the economic values commonly attributed to birds center around their services in eating unwanted insects or other unwanted things. For many years, *economic ornithology* was practically synonymous with *food-habits study*. An imposing list of other economic values applicable to birds appears, nevertheless, and for convenience they have been classified as follows (Wing, 1951):

POSITIVE VALUES

- Esthetic (nature study, their presence)
- Recreation (bird watching, hunting)
- Useful products (food, wearing apparel, manufactured articles, down, fertilizer)
- Useful activities in the wild
  - Control of plants and animals
  - Distribution of plants and animals
  - Scavenger service
  - Health protection (control of disease carriers, such as rats and mosquitoes)
- Sources of employment (ornithologists, naturalists, teachers, protectors)
- Crop saving
- Useful activities in confinement (experimental birds, domestic birds, trained birds, exhibits)

NEGATIVE VALUES

Destruction of property
Competition with or predation upon "preferred" animals
Distribution of unwanted plants
Encouragement of undue trespass

FOOD HABITS

Food Habits Study. The study of bird food habits arose from the natural desire to know more of birds and especially the economic desire to know how birds influenced crops and other interests of man. The stomach contents have long been used for study of food habits. For correct procedure, however, food habits must be studied not only by means of foods eaten but also by observation of habits, study of food availability, and determination of the bird's place in the ecological picture.

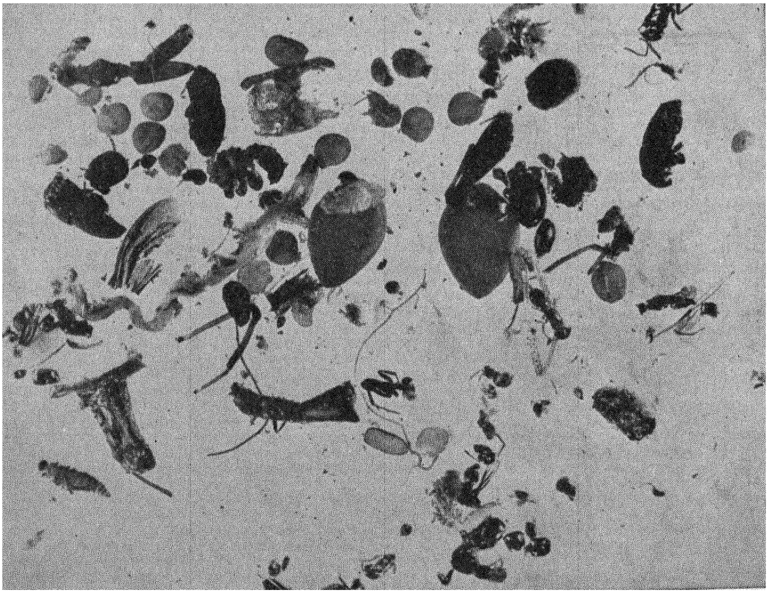

Fig. 23.1. *The remains from several American Robin droppings. This illustrates the ease with which identification of food items can sometimes be made. Cutworms, grasshopper fragments, larval European elm-leaf beetles, ants, various carabid elytra, entire weevils, cherry seeds, blue nightshade seeds, and honeysuckle seeds can be recognized.* (*Photograph by William J. Hamilton, Jr.*)

In addition to analysis of stomach contents (including sometimes the entire digestive tract), biologists use pellets (indigestible parts regurgitated by predators, insectivorous birds, and some others), and fecal droppings (Fig. 23·1). The hard parts of insects, seeds, bones, and scales usually are identifiable. Sometimes also feathers, hair, and soft parts can be distinguished. Even needles and leaves, along with parts of some other vegetation, may be identified by structure. For this analysis of food items, the stomachs are preserved dry or wet—usually dry for grain and seed eaters, in formalin usually for soft foods and animal parts. The material to be examined is spread out and studied under a low magnification. Suitable samples of seeds, bones, hair, or feathers are needed from time to time for comparison. Keys and published descriptions of seeds, bones, hair, and feathers prove useful.

The amount of each item eaten is reported in several ways, choice being governed by species, the kind of food, kind of research being made, and, with little doubt, the preferences of different ornithologists. The most commonly used measures are by weight, volume, frequency of occurrence, number of each item, and per cent of the whole.

Food Adjustments of Birds. The food habits of the bird and the food needs of its body have become adjusted through evolutionary processes. The bird has evolved a digestive system and physiological constitution for using foods of a narrow or wide choice, as the case may be. The feeding instincts and structural capabilities ordinarily determine a bird's choice of foods. (Availability, however, may determine what it can get.)

The Short-eared Owl, for example, has an instinct to prey upon rodents, talons with which to seize them, a bill for tearing the prey, flight (noiseless) with which to seek food, eyes with which to see in the dark, and a digestive system to make the food available for the blood stream to distribute throughout the cells of the entire body. An Owl coursing over a stubble field (in the daytime if need be) will not be attracted by the shattered wheat kernels and weed seed, though a Slate-colored Junco will. A meadow mouse feeding on the wheat or weed seed will release a feeding (i.e., preying) reaction in a hungry Owl but not in a hungry Junco. The grains and seeds, on the other hand, will release the feeding reaction in the Junco but not in the Owl. A truly intricate system is the bird in relation to its food. Feeding goes on so regularly, however, that one rarely appreciates the complex actions working so smoothly together. Even this brief account hardly indicates its ecological nature, the step-by-step meshing of innumerable biological cogwheels (Chapters 10, 11).

Food Consumption. As a general rule, birds eat a greater amount of food pound for pound of body weight than other organisms. But very great differences in the available calories of various foods make direct comparisons difficult. While meat amounting to 1 or 2 per cent of the body weight might alone be enough daily food to sustain a moderately active man, evidently no bird could get along on so little. In general, the bird consumes more food because it lives a rapid life, has a high temperature, and has a small body.

Table 23 • 1

Daily Food in Relation to Body Weight

Species	Body Weight (Grams)	Daily Food in Per Cent of Body Weight
Domestic Goose	1800	3.4
Common Buzzard	855–900	4.5
Pigeon	516	5.4
Tawny Owl	442–475	5.0
Pigeon	360	6.5
American Sparrow Falcon	200	7.7
Lapwing	195	7.8**
Little Owl	164–172	5.5
Dove	160	8.6
Bob-white	170	8.8**
English Blackbird	118	7.3**
Dunlin	114	8.5**
Mourning Dove	100	11.2*
Song Thrush	89	9.8**
Chaffinch	22	13.2*
Great Titmouse	18	26.0**
Redbreast	16	14.7**
British Goldfinch	13	17.5*
Blue Titmouse	11	30.0**

* Seeds and grains.

** Dry weight of meal worms (estimated at 40 per cent of live weight).

Data on European birds from Margaret Morse Nice, "The Biological Significance of Body Weight," *Bird-Banding*, 9(1938):1–11.

In the discussion of the *Bergmann Rule* earlier (page 185), mention was made of the fact that larger birds with their lower bulk-to-surface ratio tend to have the advantage over their smaller fellows in colder regions. This advantage evidently lies partly in the difference in relative metabolic rates (perhaps reflecting surface areas). Metabolic rate is reported to vary among experimental animals approximately with the two-thirds power of body size (page 83). How this would compare with birds in the wild is not known; but one should expect the difference to be similar. Data on the percentage of food eaten relative to weight of the bird show (Table 23·1) an increase in food with decline in body size (Fig. 5·7). A bird eats more in cold weather when energy demands are high than in hot weather (page 86). Measurements of birds in Europe indicate that the difference can be very great for different temperatures. That larger birds can get along on proportionately less food than smaller ones is also shown in Table 23·2.

Table 23·2

Daily Food Consumption in Relation to Body Weight and Temperature

Species	Body Weight (Grams)	Food Consumption in Per Cent of Body Weight at		
		65° F.	48° F.	45° F.
Masked Weaver	40	20	25	28
Red-billed Weaver	18	28	30	33

Source: Margaret Morse Nice, "The Biological Significance of Body Weight," *Bird-Banding*, 9(1938):1–11.

As would be expected, the amount of food consumed will vary with its nutritional value (page 256). In general, animal foods supply more usable calories for each unit than do vegetable foods. Seeds and grains of various kinds are somewhat less concentrated than animal foods, though some seeds are more concentrated than some animal foods. Fruits tend to be more nourishing than leafy foods such as the grasses eaten by grazing Geese.

Designation of Birds by Food Habits. For convenience, food habits serve as the basis for grouping many common birds. Birds within these groups have somewhat similar habits and structures owing to their similarity of food choice (see Chapter 3):

Carnivorous, meat-eaters
Herbivorous, plant-eaters
Frugivorous, fruit-eaters
Omnivorous, eat both plant and animal foods
Insectivorous, insect-eaters
Granivorous, seed-eaters
Piscivorous, fish-eaters

Because more than eight thousand species of birds spend so much of their waking lives looking for something to eat—in competition with each other, with others of their own kind, and with other animal life—we need not be surprised therefore that a tremendous variation in food habits exists. In a sense, for everything edible, there is some bird to eat it (either first- or secondhand) but with some notable exceptions. Few or no birds feed primarily upon some readily

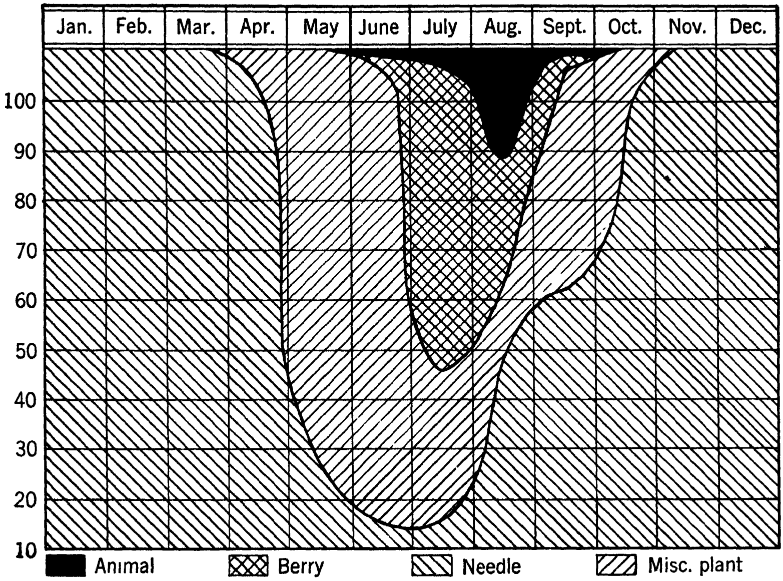

Fig. 23·2. *Graphical representation of the food of the adult Blue Grouse, a "conifer forage feeder" which obtains nearly three-quarters of its yearly food from needles. The figures represent percentages of the total eaten. This illustrates a commonly used method of showing food habits. (By permission from* Practice of Wildlife Conservation, *by Leonard W. Wing, p. 144. Copyright, 1951, John Wiley & Sons, Inc., New York.)*

and widely available vegetation. The oak, maple, and other deciduous leaves of the forest, for example, are eaten but little by birds; none use them as a staple food. The same applies largely to other "forage" of the field, brush, and forest. A few gallinaceous birds eat the leaves of some plants, sometimes in great quantity. Sage Grouse live for long periods almost exclusively upon leaves of the desert sagebrush (*Artemisia*). Geese may graze, but for the most part, birds leave this food supply to the rabbits, rodents, ungulates, and insects.

Almost no mammal and but a few Grouse (*Dendragapus*, *Canachites*, *Tetrao*, *Falcipennis*, and sometimes *Lyrurus*) eat so many conifer needles that needles form a major portion of their diet. In a sense, they are "conifer forage" feeders, a rarity in the entire vertebrate world (Fig. 23·2). Naturalists afield may wonder justly at the seemingly remarkable fact that among the vertebrates, only the Tree Grouse and two rodents have taken to conifer forage, one of the world's great vegetational resources, as a staple diet.

Among birds with interesting kinds of food habits may be mentioned the Everglade Kite that feeds solely or nearly so upon snails which it extracts from the shell by its specially adapted habits and bill (page 426). The Dovekie feeds upon crustaceans floating on the surface of the open sea; in times of rough weather, the floating life goes deeper into the water and Dovekies go hungry. The Harpy Eagle of Tropical America preys upon the upside-down sloth, and an Eagle in the Philippines preys upon monkeys. Yet in the course of a year, a variety of birds may feed in a single tree or bush, each to its own taste: the Ruffed Grouse on buds in winter, New World Warblers upon leaf-eating insects in summer, Hairy Woodpeckers upon wood-borers the year around, Black-capped Chickadees upon insects hiding in the bark, Yellow-bellied Sapsuckers upon sap, Cedar Waxwings upon the fruit, and perhaps a Ruby-throated Hummingbird upon the nectar of the flowers. Some of these birds may be designated as insectivorous, but others cannot be confined to any fixed listing. Some may be rather rigidly limited in their dietary and others can choose rather more freely.

Methods of Feeding. Because the structure and physical nature of the bird relates so intimately to its feeding habits, the methods of feeding are necessarily subject to these structures. Among some species, the food habits clearly retain much that may be interpreted as of ancestral character. Most groups of the fish-eaters, for example, have probably descended from long lines of fish-eaters. But the Kingfishers, though fish-eaters, are related not to the other fish-eaters but to land birds not feeding upon fish. During their long history of fish eating, birds have developed various ways of catching their prey. The Kingfisher often sits upon a perch and waits until a fish appears

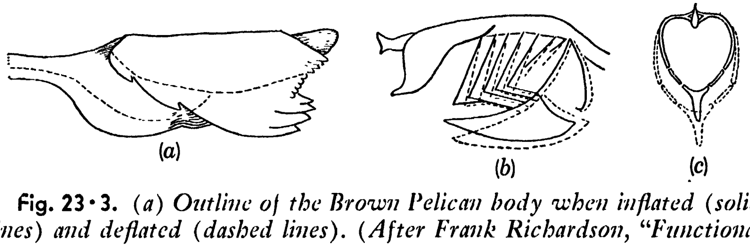

Fig. 23·3. *(a) Outline of the Brown Pelican body when inflated (solid lines) and deflated (dashed lines). (After Frank Richardson, "Functional Aspects of the Pneumatic System of the California Brown Pelican,"* Condor, *41 (1939):16.) (b) Lateral and (c) frontal views of a bird to show expansion of body by inhalation (dashed lines) and contraction by exhalation (solid lines). (After A. W. Schorger, "The Deep Diving of the Loon and Old-Squaw and Its Mechanism,"* Wilson Bulletin, *59(1947): 238.)*

before flying and plunging from the air for it. The Brown Pelican flies low over water, locates a fish, tips up to a stall, then plunges after it. The pneumaticity of its body absorbs the shock and probably helps it to ride high in the water (Fig. 23·3).

True divers, as distinguished from the plungers, go under from the surface by their own effort, not from momentum gained in the descent through the air. They have considerable capacity to expand and contract the body, which with lowered pneumaticity of the bones, gives reduced specific volume (Schorger, 1947), a necessity for efficient submarine life (Fig. 23·3). Careful timing by an alert and ingenious bird watcher along an English shore established the principle of *time-depth ratio.* If the time under water of three successive dives be averaged for bottom feeders, the depth of the water will be found roughly by allowing 20 seconds for the first fathom (6 feet) and 10 seconds for each additional fathom (Dewar, 1924). Among Coots, the rule is 10 seconds for the first and 10 seconds for

Fig. 23·4. *The Black Skimmer feeds by skimming over the surface of the water with its lower mandible cutting the surface. The wake from the bill of the bird on the right shows clearly. (Photograph by Ivan R. Tomkins.)*

each additional fathom. The Great Blue Heron and its relatives obtain fish by standing in the water and seizing them. The Black Skimmer passes back and forth over the water, its longer lower mandible cutting the surface, ready to seize its prey (page 43, Figs. 3·9, 23·4).

Few birds unable to go under water by diving or plunging have much ability to seize fish unless from above, as in the Heron or Skimmer. The Waterfowl that feed by dabbling or tipping up in shallow waters, such as the Mallard, Swan, or Goose, have low fish-catching capabilities. Yet a number of interesting fishing traits have been reported, like that of a Horned Owl waiting at a hole in the ice or of a bird seizing a catfish gulping air at the surface.

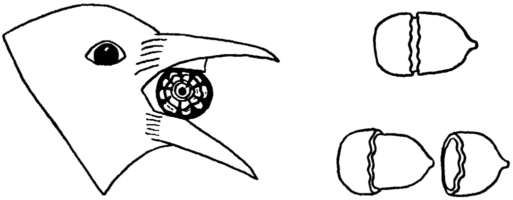

Fig. 23·5. *The Bronzed Grackle opens acorns by rotating them in the bill and pressing the shell against a ridge in the palate. This cuts the acorn shell and exposes the meat. (After A. W. Schorger, "The Bronzed Grackle's Method of Opening Acorns,"* Wilson Bulletin, *53(1941):238.)*

Also, other food habits of birds sometimes hinge upon one structural possession. Among Passerine birds, hardly anything seems so startling to an observer as to watch a Bronzed Grackle open an acorn with its "buccal lathe" (Fig. 23·5).

Choice of Chief Food. The adjustments of a bird to its food sources include choice of foods in sizes that it can eat, as well as foods that the body needs or can use. Its discrimination, however, may be largely between wholesome foods and others. *Structural* limitations, both upper and lower, prevent many birds many times in their lives from feeding upon foods otherwise suitable. The Bob-white can eat small acorns whole, and the meats of larger ones if a Bronzed Grackle or Blue Jay has opened and lost them. Structural inadequacy limits the Bob-white in its use of acorns but not a Grackle. A Golden Eagle has the power to seize and eat a marmot on a cliff, but a Shrike does not. An Osprey can feed upon large fish, though a Common Tern must be satisfied with minnows. Yet even an Osprey can make a mistake and sink his talons into a fish too large.

It would hardly pay the Golden Eagle to feed upon grasshoppers as a regular diet, but it does prove profitable to the American Sparrow

Falcon. The Golden Eagle can hardly afford to feed upon small rodents, but in times of abundance, he might find it profitable to feed on them in a sort of "mass consumption" manner. More than one hundred thousand primrose willow seeds were found in the stomach of a Mallard Duck (Henderson, 1927), but no Mallard can long survive on such foods if it must pick them one by one. A Slate-colored Junco, however, could perhaps do so. The Mallard can use small seeds by eating seed heads, a form of mass consumption. Under stress of food shortage, however, a bird may feed upon many foods not suitable for sustaining life for long.

Biologists studying the food habits of game birds often classify winter foods as *preferred*, *staple*, *emergency*, and *stuffing*. Birds depend upon the staple foods for energy and heat, especially in cold weather, though they may not supply a balanced diet. Except for some animal food, probably no single food item can itself supply a balanced diet.

Within the limits of its innate food choice, an animal seems to govern its eating by the abundance of foods available. The exact kinds of seeds and berries eaten by a White-throated Sparrow may differ from area to area according to what is available. In the Lake States, White-throated Sparrows may feed extensively on berries of the elder (*Sambucus*), and on those of the yaupon (*Ilex*) in the winter range in Texas. The famed incident of the California Gulls of Great Salt Lake feeding upon Mormon crickets in 1848 illustrates the way abundance may influence food choice. For this service to hard-pressed pioneers, a grateful people erected a notable monument in 1913 at Salt Lake City, Utah.

Foods of Special Need. We know almost nothing of specific nutritional needs of the wild bird's body, a subject to which human beings pay so much attention, especially for vitamins and minerals. The need for grit in the gizzard forms one definite use of minerals, but grinding material seems always to be in suitable supply before its loss might be critical to the bird. Even hard seeds will serve as grinding material (page 62). Presumably the bird with a free dietary choice gets all the minerals that it needs, though such a concept tells little and assumes a lot. Animal-food eaters seem likely to get all the dietary necessities from the bodies of their victims. Perhaps many birds can synthesize some vitamins within their own bodies.

Eggs of wild birds always seem to have sound shells, and bird bones usually seem well made, which gives rise to the assumption that calcium in sufficient quantity and form is not lacking to birds. Yet careful study in the wild of eggs and perhaps x-rays of birds might show some deficiencies. A few birds seek salt, but this habit may not necessarily indicate that their bodies need it for proper functioning (page 92). Many of the same species live where such salt is not known to be available. (Even access to salt in wild mammals like the elk appears not essential, though the animals relish it.) Birds especially attracted to salt are some of the Finches (Red Crossbill, White-winged Crossbill, Purple Finch, House Finch, Evening Grosbeak, Pine Siskin) and Doves (Passenger Pigeon, White-winged Dove, Mourning Dove, Band-tailed Pigeon). The Band-tailed Pigeon chooses to drink salt water at the margin of Puget Sound mud flats even though freshwater streams are available (Neff, 1947).

Food Storage. Cases of actual food storage are rare among birds. The Blue Jay, Steller Jay, Red-headed Woodpecker, and several other American birds put acorns in holes and crevices. Probably this is true food storage. Nuthatches will take pieces of food, such as suet at a winter feeding station, and tuck it into crevices in the bark of trees. Shrikes impale insects and occasionally small birds and mice on thorns. But this seems mostly for convenience in feeding, because they have no talons, rather than an example of food storage in the true sense.

ECOLOGICAL-ECONOMIC RELATIONS

Food Chain and Food Web. Because the sun is the only original source of biological energy available, its transfer to the bird involves a complicated series of channels. Plants entrap the energy by photosynthesis and combine it with water and sometimes other substances (page 198). The energy passes on to a herbivorous feeder that stores it within its own body. The next transfer is to an animal that feeds upon the plant-eater. The transfers from thence onward are from an animal-feeder to another animal-feeder. To this system of energy

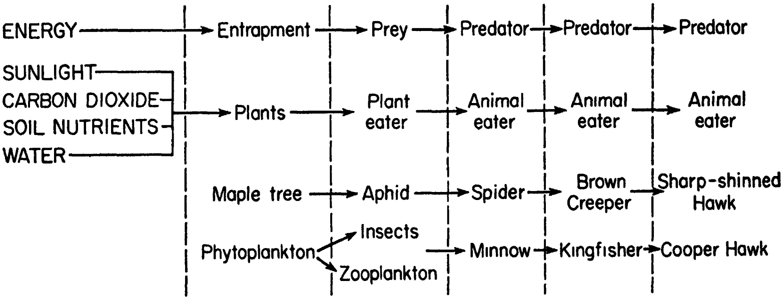

Fig. 23·6. *Diagrammatic representation of the food chain and an example in land and water habitats.*

transfer is given the name *food chain*, to each stage the name *link* (Fig. 23·6). The several food chains in an environment form a *food web*. Seldom does a food chain exceed four or five links, except for *interpredation*, the preying of predator upon predator.

The food base involved in predator-prey relations has been given special attention (Errington, 1946). The listing of the bird and animal life of an area by numbers shows that it varies from a large number of some, such as rodents and songbirds, to a few of the larger predators. This ecological listing as a table in order of numbers has been called a *pyramid of numbers* (Leopold, 1933).

Insect Suppression. Many factors cause mortality in insects or prevent them from developing, including malfunctioning in the insect itself, but the most important are believed to be the favorable and unfavorable aspects of the habitat. Among the immediate factors is climate, demonstrably the most important single one. Birds play an important general role and often an important specific one. Birds have many alternate foods, both insect and noninsect, so that local extermination of any one usually still leaves them a food base. This versatility measurably increases their usefulness to man and his crops; through this, they tend to apply pressure upon the insect life in proportion to insect abundance. By that token, the birds stand ready to prey upon any and all insects. Their general tendencies measure their usefulness (not just their specific activities)—the constant restraint that they place upon insect life, not just their more spectacular actions during outbreaks. Even so, the highly mobile bird gathers quickly in numbers at the scene of an outbreak. The number of birds that feed upon grasshoppers and locusts during an outbreak has been found to be very large. Two hundred two species fed upon locusts and their eggs during the great invasion of Rocky Mountain migratory locusts into the western prairies and plains from 1873 to 1876 (Henderson, 1927). The Loggerhead Shrike is one of the birds that will turn to such insects or feed upon them regularly. It leaves signs of its work by impaled insects on thorns and even on barbed wire (Fig. 23·7). But in the highly artificial environment under the conquest of man, the natural checks upon insects may not be sufficient, and artificial control efforts may be needed also.

The insect-feeding habits of birds long have been investigated. Certain birds may be the chief ones controlling some insects. The Woodpeckers feed upon bark beetles, and foresters in the southern pine belt have considered them about the only control likely to be effective without costing more than the value of the timber saved. A family of Bob-whites in a potato patch will keep it free of potato beetles. Observation of an infestation on a single small mountain ash tree in the Adirondacks showed that one Veery with a nearby nest completely cleared it of leaf-eating insect larvae that had defoliated more than 10 per cent of the tree before being found and destroyed by the Veery, evidently to the last one.

Such examples have occurred innumerable times, and the important role of the birds has been demonstrated clearly. Yet it would be unrealistic to accord to birds the all-controlling role as crop protectors envisioned in such statements as, "If the birds were all destroyed, agriculture in the United States would instantly cease." But the insect-suppression value of birds to agriculture clearly runs into the hundreds and even thousands of millions of dollars yearly.

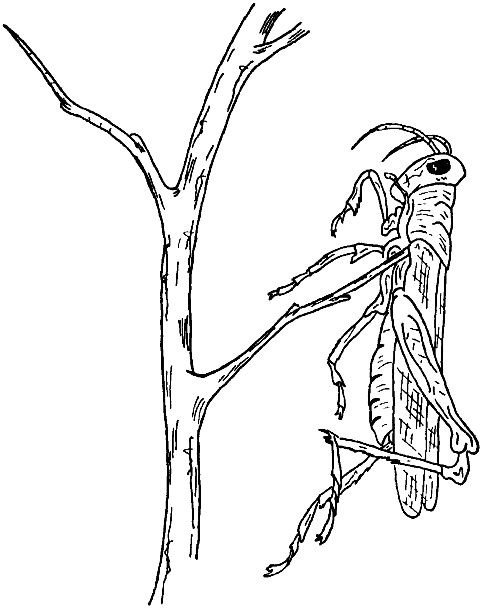

Fig. 23 • 7. *The Loggerhead Shrike, in common with others of its family, impales its food upon thorns.*

Insecticides and Birds. The widespread use of insecticides, especially in broadcast and airplane spraying, poses yet another problem for the birds. A low concentration of spray seems to cause little harm, but 5 pounds of DDT to the acre in a Maryland scrub woods reduced the five commonest birds by about 65 per cent; only the Chat was uninfluenced (Robbins and Stewart, 1949). In other studies, 3 pounds of DDT to the acre markedly reduced the number and vigor of young House Wrens when applied during the hatching period (Mitchell *et al.*, 1953).

Because differences in resistance to acute and chronic poisoning have been noticed in experimental animals, similar conditions no doubt occur in wild birds also. The rapidity with which chemists turn out new insecticides out-distances knowledge of their influence on birds; it also out-distances knowledge of their influence upon the health and well-being of man himself. The hazards to human health of more than two dozen new insecticides (Webster, 1951) indicate clearly a danger to birds in the wild as well.

Birds and Plant Distribution. That birds can serve as the distributing agents for many plants seems demonstrated, though how many plants and which birds are less definitely known (Henderson, 1927). Many seeds have been tested for viability after passing through the alimentary tract of birds, even of granivorous ones, and a surprising number germinate. Throughout the range of red cedar (*Juniperus*), yaupon (*Ilex*), grape (*Vitis*), nightshade (*Solanum*) and Poison Ivy (*Rhus*), for example, the seeds passed in the droppings of birds sprout under isolated trees, along fence rows, and under telephone wires where only an animal like a bird could have deposited them.

Few plants depend directly upon birds for seed dissemination, but the various mistletoes seem to do so. The berries are eaten by the birds, which digest the covering and pass the seeds in defecation, now with a viscous coating that sticks to anything touched, especially the limbs upon which birds perch. The Cedar Waxwing in the southern states and several birds of Australia, Mexico, and the West Indies have been reported to be distributors of mistletoe (Henderson, 1927; Sutton, 1951). The heavy seeds of trees like the oaks would not be able to move up steep slopes to replace trees higher up, and producers of such heavy seeds need the services of "uphill planters," even though only once in centuries would their services be absolutely essential in planting a seed to replace a tree (Grinnell, 1936).

Birds have been reported to disseminate various blights, but this seems of little importance. Spores of the chestnut blight, for example, were found upon the plumage of nineteen species of birds, the greatest abundance being upon the Downy Woodpecker (Heald and Studhalter, 1914). But this influence compared to that of wind was deemed not very important except perhaps for "spot infections."

A few plants, chiefly tropical, depend upon birds for pollination (hence, they are termed *ornithophillus*), primarily by Hummingbirds. The bird feeding at a flower brushes pollen upon its plumage, which then may be transferred to another plant or to other flowers of the same plant (Fig. 23·8).

The enormous quantity of weed seed eaten by birds has long served as an illustration of a service to agriculture. The total eaten throughout the farming areas of the world runs into astronomical figures. Each seed eaten in a farm field is a seed not likely to sprout later, though some, nevertheless, will pass through the bird in a viable condition.

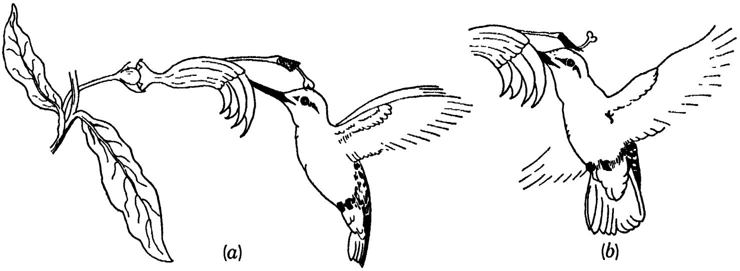

Fig. 23·8. *Hummingbird feeding from a flower* (Centropogon cordifolius). *During the early flowering stage* (*a*) *pollen from the antlers gets on the bird's crown; the pollen rubs off* (*b*) *on to the stigmas of flowers in a later flowering stage.* (*After Helmuth O. Wagner, "Food and Feeding Habits of Mexican Hummingbirds,"* Wilson Bulletin, *58*(*1946*)*:69–93.*)

Predation Upon Rodents and Other Mammals. The good services of Hawks, Owls, and other predatory birds as controllers of rodents goes rather unnoticed compared to the publicity attending a single event considered by some a "misdeed" (see also Chapter 22). In general, a Hawk or Owl preying upon rodents should be counted as worth no less to a farmer than a hen in the Chicken run. Particularly is this true of the western lands where rodents feed extensively upon forage useful to livestock. A Short-eared Owl of the British Isles would probably eat between 95 and 142 pounds of field mice in a year (Chitty, 1938). Comparable service should be expected elsewhere in the world.

The Great Horned Owl is one of the few winged predators feeding at night physically capable of holding feral house cats in check. It also makes it well nigh impossible for brown rats to live away from buildings in the Northern winter. An extremely interesting and much cited incident indicates the inherent value of the Owl in rodent control. Cats locked up overnight in the storage cellar of a brewery fled in terror when the doors were opened next morning. But an Owl similarly locked up killed nine rats the first night and soon cleaned out the rest (Henderson, 1927). Incident upon incident have been related—and many more can be—to illustrate the point: enter Hawk or Owl, exit mouse or rat.

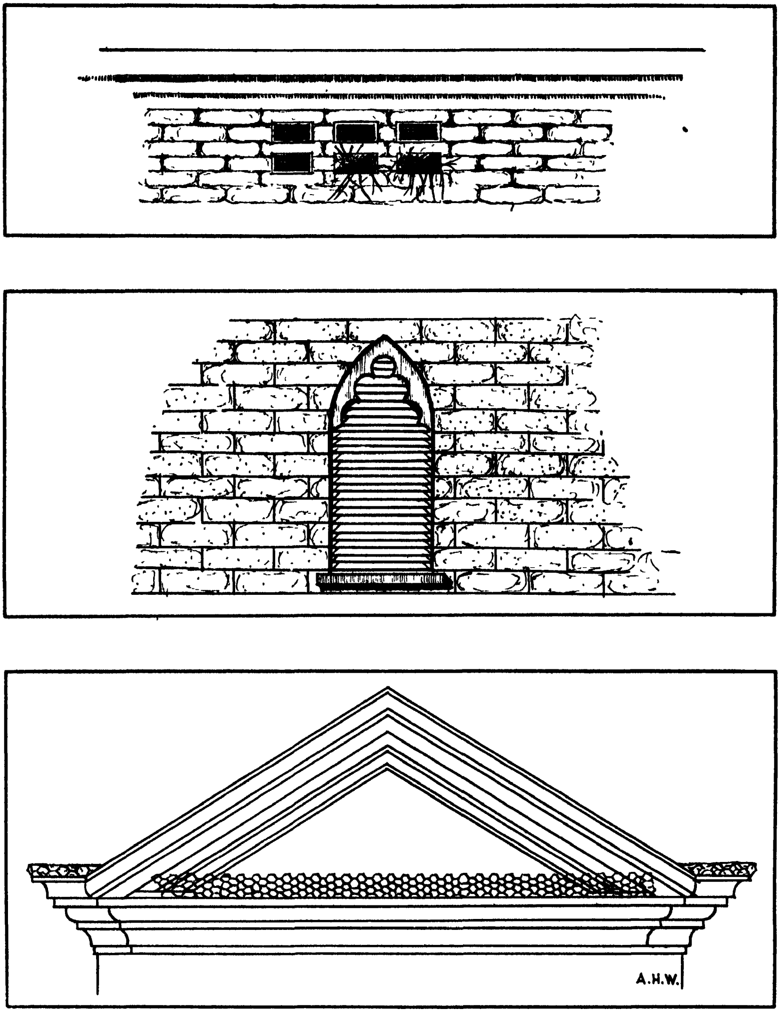

Fig. 23 • 9. *Screening prevents birds from perching on buildings or nesting in ventilators. (By permission from* Practice of Wildlife Conservation, *by Leonard W. Wing, p. 308. Copyright, 1951, John Wiley & Sons, Inc., New York.)*

Bird Damage. A biological axiom holds that animals living beyond their native range or in ranges invaded and seriously degraded by man may at times conflict with man's preferential interests. The preying by predators upon game birds, game mammals, and game fish in America cannot correctly be classified as a "damage," because wild animals are not the property of the individual nor are they the subjects of commercial or private use except as a privilege from the public.

Red-winged Blackbirds have been found to injure corn and other grain crops; careful studies have shown that acetylene exploders will protect 10 acres of corn while eighteen half-yard square cloth dangles will protect about an acre (Cardinell and Hayne, 1945). Acetylene exploders have also been used successfully to protect orchards from many birds. Flashing bottles and tin or aluminum sheets have worked well; whirling or twisting shiny streamers have proved better. All seem to be as good as the traditional scarecrow and sometimes much better.

The largest popular complaint, however, is directed at birds about buildings and city trees, chiefly against those European immigrants: the Pigeon, Starling, and House Sparrow. The Starling has proved an especial pest in a number of cities where the birds roost on the ledges and projections of buildings and in trees. Its role as a pest should be reason enough for all the strong aversion and controls against importing or transplanting any other animal. Various methods have been tried to evict them, often at great cost—scarecrows, Owl cutouts, lights, shakers, gas, poison, shooting, fireworks, water hoses, nets. Recorded fright calls played back near the roosts proved effective in evicting Starlings (Fings and Jumber, 1954). But the most permanent results come from preventions: filling in or sloping ledges, plugging holes, and screening perching places (Fig. 23·9).

DOMESTIC USE OF BIRDS

Of all the several thousand species of birds in the world, barely a handful have been used by men as domestic stock. For practical purposes, they are here listed in three groups: (1) captives, (2) slaves, and (3) domestic ones. To be truly domesticated, an animal must be broken completely to man's will, psychologically as well as physically. This has not happened often. In addition to domestication, some commercial use may be made of wild birds, chiefly through commercial products.

Bird Captives. Caged birds, popular with some people and unpopular with others, include a wide variety. But the largest number come from three groups: (a) Parrots, Lories, Macaws, and Cockatoos, (b) Starlings and Mynahs, and (c) Canaries, belonging respectively to the families Psittacidae, Sturnidae, and Fringillidae. Many wild birds have been made captive for their ability as songsters (Canary, Mynah), as imitators of human sounds (Parrots, Mynah), and as objects of curiosity (Parrots, Lovebirds, Macaws, Cockatoos). Canaries inhabit the Canary and adjacent islands (whence the name). People raise them by the thousands throughout the world in various "breeds." Mynahs inhabit much of the Old World, but those used as cage birds live wild in India and adjacent regions. The so-called "Talking Mynahs" are usually captive Hill-Mynahs.

Several members of the Parrot group appear in captivity from time to time, some because they can crudely imitate human speech, others because of their bizarre looks or curious habits. The ones chiefly on the market are the Australian and African Lovebirds, the Gray Parrot, Green Parrot, Yellow-headed Parrot, and Macaw of the Neotropical realm, and the Cockatoos of the Australian region. But any highly colored members of the family may be looked for in captivity, especially in their native range. From time to time in various parts of the world, other caged birds may be found.

The Ostrich, athough not strictly a caged bird, has been raised on farms for some years, the first during modern times in the middle of the nineteenth century. Hence, raising Ostriches for their plumes may be a recent use of birds.

The Peafowl, also not strictly a caged bird, lives wild in Ceylon and India; the captive stock came into the western world at some ancient time. The principal use of the Peafowl is as an attraction in parks and about houses.

Bird Slaves. A "slave bird," as distinguished from captives, is one that is forced to "serve" men. The Falcons, Hawks, and Eagles used in falconry are such slaves to the falconer. In earlier England, belts were drawn about the neck of tamed Cormorants to prevent them from swallowing fish. When turned loose in the water, they caught fish but could not swallow them. Because of training, they came to their keeper who by manipulation of the throat, forced removal of the fish. In parts of the Orient, Cormorants serve likewise. In some Pacific Islands, Man-of-war Birds have been used to carry messages somewhat as Pigeons have been used elsewhere. Few other slave birds have been used except as decoys (e.g., the "stool pigeon" of Passenger Pigeon days).

Major Domesticated Birds. Only four birds can be considered of major commercial importance: Chicken, Turkey, Goose, and Duck.

Primitive man domesticated all of them in some unrecorded time long ago.

Chicken. The Domestic Chicken developed from the Jungle Fowl of Southeast Asia and adjacent islands. It seems to have come into the western world, probably through Persia, at least by B.C. 500. Many varieties have been developed, some of which antedate its coming into the West; of this number, about a score are of importance. In its native life, the Jungle Fowl seasonally lays in sets of perhaps a dozen eggs. Some authorities say that it may be monogamous, others polygamous.

Turkey. The Conquistadors found the natives of Mexico raising a large gallinaceous bird that they took back to Spain with them. It soon acquired a name, presumably from its call or the fancied resemblance of its head to the fez worn then by the Turks. Later this type of Turkey was brought back across the ocean. The domestic Turkey, however, comes not from the Wild Turkey that lived in New England, greeted the Pilgrims, and graced their Thanksgiving table; it comes from those domesticated by the Indians of Mexico, who, along with their fellows of Central and South America, appear to have an aptitude for taming wild birds and mammals.

Goose. Though we cannot be exactly certain of the species that served in ancient times as the source of our domestic birds, the common Graylag Goose of Europe appears to be the ancestor of most breeds. The Graylag ranges widely over the Old World and breeds over much of the northern part. It doubtless was domesticated or kept half-tamed by early man, probably prehistoric, in the same way that American Geese have been kept in captivity in the past. (It must be remembered, however, that the laws and regulations of Canada and the United States discourage the keeping of native birds in captivity.)

Domestic Geese have changed surprisingly little from their wild progenitors. A number of different breeds have been developed; the most strikingly different from the Graylag are the white ones. Like most domesticated animals, the Goose has increased in size and lost much of its inherent wildness. But like some others, its breeding season is still substantially that of its wild ancestor.

Duck. The several breeds of the common Duck are all descended from the common wild Mallard of Europe, a bird closely related to the New World Mallard. Many of the breeds (e.g., Indian Runner, Pekin) have departed rather greatly from the Mallard type. The exact time of domestication is unknown, though there is little doubt that primitive man did the domesticating.

Minor Domesticated Birds. Four birds may be listed as minor domestic ones for the simple reason that raising them in domestication is infrequent and they are not very important commercially or the industry has not become concentrated anywhere as compared with the major ones.

Among these is the *Swan*, descended from the Old World Mute Swan. Just as in the case of other domestic birds, the time of domestication is in doubt. Though once raised for the table, Swans today are kept chiefly in parks and on estates. Occasionally tamed Swans other than the Mute appear as captives. When Swan-raising flourished on the Thames, in order to distinguish the birds, distinctive marks of ownership were required upon the bills, which "swan-marks" were recorded by the Royal Swanherd. (In like manner, cattle on the western ranges today carry identifying brands, which are registered in an official brand register and checked by brand inspectors.)

The *Muscovy Duck* was domesticated by the Indians of Central and South America at some unknown time in the past. (Its range in the wild reaches almost to the Rio Grande in Mexico.) Though it is raised in domestication, the number is not large compared with other Ducks.

The *Guinea Fowl* of Africa seems to have been domesticated by natives of the Guinea Coast of Africa and probably introduced into the civilized world by the Greeks or Romans, but certainly before the fifteenth century. Guinea Fowls are raised mostly as curiosities, though some are raised as a delicacy. They have changed little by domestication.

All our breeds of the Pigeon or Dove probably have developed from the common *Rock Dove* of the Old World. Yet its ancestral relationship and home are somewhat in doubt. Although it is not certain, it seems unlikely that much admixture of blood from other species has occurred (page 398). Pigeons are raised as curiosities, for the table, for carrying messages, for racing, and for experimental use. There are some two hundred different breeds.

Commercial Products. No commercial uses any longer may be made of wild birds in the United States and Canada, though elsewhere commercial uses are practiced. The protective tradition of the United States and Canada may in time become established in other regions of the world.

Probably the best-known commercial use of all, the guano industry, is not a commercial use of the bird itself but of its excrement. Bird guano accumulates in arid regions where birds nest in colonies (Hutchinson, 1950). Rich, cold, upwelling ocean waters supply quantities of marine life. The bird islands of Peru (Murphy, 1925) particularly have been noted for guano, and the industry has been organized and controlled on a management basis. Many chemicals occur in guano, but the principal ones for fertilizer are nitrates that may reach 26 per cent and phosphates that may reach 18 per cent but in inverse relations with each other. In actual practice, the guano birds bring back to shore in a relatively small way some of the fertility washed to sea by the rivers.

In South America lives a most interesting bird, the *Guacharo*, called also the Oil-bird (Steatornithidae), one of the few night-feeding fruit-eaters in the world. When the very fat young are about two weeks old, natives gather them from their nests (usually in caves) and render them for a colorless cooking and illuminating oil. (The birds living in caves are believed to use acoustical orientation.) The Great Auk gave oil when its body was tried out, but it was pursued also for eggs, meat, and skins. The Penguins too have from time to time suffered pursuit for oil, the tried-out carcasses serving sometimes to heat up the rendering kettles for others.

In some parts of the world, though not in America, people raid sea bird colonies for eggs to eat (Cott, 1953). Often the colonies are systematically "egged" from the beginning of the season on, which gives the eggers some assurance of relatively fresh eggs.

The feather trade for millinery purposes made a number of birds extinct or nearly so, the Egrets along with others. The cutting off of the American market by prohibition of importation of millinery feathers (Tariff Act of 1913) stopped most of the destruction, though it has continued in out-of-the-way places and in a few backward areas. Any source of legal feathers (other than from poultry) is bound to be small (such as Ostrich farms).

Few bird feathers have been used for clothing except in trimming, though Indian medicine men and others used them for ceremonial costumes and decorations. Montezuma's headdress (perhaps actually a cloak) was of this nature. The cloak of King Kamehameha of Hawaii was made of feathers from the Mamo. Eskimos may use skins of Eider Ducks for making clothing.

In some lands bordering upon the North Sea, North Atlantic, and Arctic Ocean, people collect the *down* from Eider Ducks (mostly from the nests) and sell it, the eider down of commerce. Because to a people living a marginal existence it forms an item of income worth going after, considerable protection accrues to the nesting birds that more may nest and that more down may be collected.

The ancient and primitive use of birds as medical nostrums surely should not go unnoticed. The meat of the English Robin and Hedge Sparrow, for example, was deemed effective in the Middle Ages for elimination of stones and other obstructions of the urinary system (Lack, 1946). When made into a powder by drying and burning, it was considered to be as effective as eating of the meat itself, which seems highly probable. Even some bird dung was thought to have medicinal properties.

SUGGESTED READING

*ALLEN, ARTHUR A., *The Book of Bird Life.* New York: D. Van Nostrand Co., Inc., 1930.

AMERICAN ORNITHOLOGISTS' UNION, *Fifty Years' Progress of American Ornithology, 1883–1933.* Lancaster, Pa.: American Ornithologists' Union, 1933.

ERRINGTON, PAUL L., "The Pellet Analysis Method of Raptor Food Habits Study," *Condor,* 32(1930):292–296.

*FORBUSH, E. H., *Useful Birds and Their Protection.* Boston: Massachusetts State Board of Agriculture, 1927.

*HENDERSON, JUNIUS, *The Practical Value of Birds.* New York: The Macmillan Co., 1927.

KALMBACH, E. R., "Field Observation in Economic Ornithology," *Wilson Bulletin,* 46(1934): 73–90.

PICKENS, A. L., "Bird Pollination Problems in California," *Condor,* 31(1929):229–232.

*WING, LEONARD W., *Practice of Wildlife Conservation.* New York: John Wiley & Sons, Inc., 1951.

*YOCOM, CHARLES, *Waterfowl and Their Food Plants in Washington.* Seattle: University of Washington Press. 1951.

24

Bird Study Afield

INTRODUCTION

Living birds in the field attract the interest of many people because of their beauty and sprightliness; the outdoor appeal inherent in them attracts many more. Their evident independence and their freedom of movement, freedom to come and go, evoke both sympathetic understanding and twinges of envy in still others. No one reason fits all people or even the same person at all times. But it seems certain that few ornithologists are so lacking in sentiment as to look upon birds as merely the sources of cold, scientific data. The simple fact remains with us always: people study birds afield because they like birds and the outdoors in which they live.

The fact that birds stir the enthusiasm makes them especially fit subjects for the rewarding avocation of bird study. Arousing enthusiasm in the course of scientific research of a more profound nature undoubtedly enhances the value of the work. Objects of research need not be dry and unattractive in order that the science in their study be profound and objective. In actual fact, science gains when scientists study their subjects with the zest of the avocational worker. The more thrilling the study, the more stimulated the mind, and the more stimulated the mind, the greater the likelihood that it will contribute more to the advancement of science. Many of the best ornithologists started out as avocational bird students, an outlook that left few in their lifetimes. Many another scientist received his scientific baptism and scholarly initiation in bird study.

As in any science, people vary in their approach to ornithology. Generally speaking, studies may be divided into two kinds: the study of problems (the common kind) and the study of principles (the uncommon kind). Problem research deals with the specific; principles research deals with the general. For successful fruition, the former requires careful pursuit of the problem, especially in its details, step by step to its ultimate solution or ultimate contribution of information. The latter requires an ability to compress details, in many fields when need be, in order to focus upon the principles involved. Because of the wide difference of outlook, conflicts arise, though not necessarily so if the difference in emphasis is kept in view.

Observation and Scientific Method. Though we read frequently of "new approach," "modern outlook," "modern research," and many similar expressions as though indicating that the methods of earlier ornithologists are archaic, the observation and experimental methods of bird study have remained surprisingly similar for many decades. The demands of accuracy, care, and precision now differ little from those of yesterday. Ornithologists of each succeeding year have a greater background of knowledge or more refined techniques and can interpret more broadly than could earlier bird students. The ornithological science of today, yesterday, and tomorrow differ primarily on which rung of the ladder they stand, not which ladder they use.

The basis of all science is *observation*, be it an observation under natural conditions or one under experimental conditions. No exactness not found in observations afield also is inherent in an observation of events under the most controlled of laboratory conditions. In the laboratory an observation and its interpretation are likely to be more complete than in the field because the significance of events concerned may be more completely understood. But the number of observations improves the validity of any interpretation. Conclusions once believed established may grow archaic when the future has unrolled new knowledge. Data once thought complete may prove incomplete as time gathers more information. But an observation of facts once correctly made will remain correct, though our understanding of it may vary.

Field observation has been the source of nearly all our information on the living bird and has been the basis for developing much of that knowledge gained from preserved or experimental material. Field observation remains the chief source of bird knowledge and no doubt will in the future as it has in the past—supplemented though it may be by laboratory study. Most field data results from *direct observation* of birds and their environment, even though some disturbance may arise from the presence of an observer. This soon passes and birds live as though no observer were about. Suitable use of binoculars, blinds, and observational skills eliminates all or most all of the disturbance arising from the observer's presence. *Indirect observation* is the reading of *sign* that tells of bird presence, its activity, and its way of life. Sign may be tracks, droppings, marks, feathers, or any one of an infinite number of things that show the action of the bird.

Measurements Afield. The development of techniques for measuring both quantitative and qualitative data marks an event in ornithological science that has given precise measurement for use in field records. Among the most important of these have been methods for measuring territory, behavior, and abundance now added to previous measurements, such as of time and space. The development of systems of measure provides field ornithology with a tool as important in its sphere as dissection in anatomy. Two observers measuring courtship performances of the same or of different species can gather comparable and completely reliable data. Of this reliability there need no longer be further question.

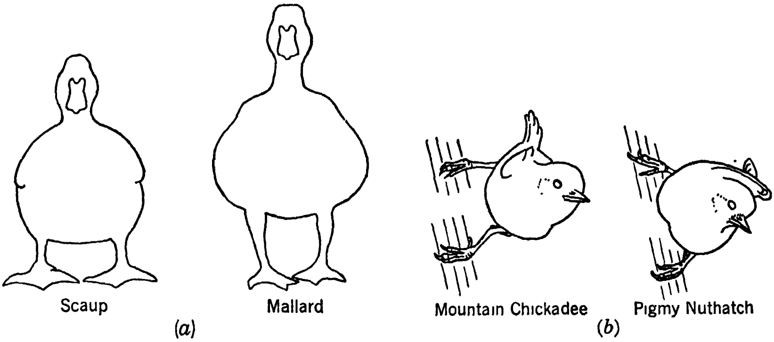

Fig. 24 • 1. *The live actions of birds may be measured and the measurements evaluated by other observers, who may also compare the measurements with others. (a) Leg position of Scaup Duck compared with Mallard. (After Jean Delacour and Ernst Mayr, "The Family Anatidge,"* Wilson Bulletin, *57(1945):24.) (b) The clinging posture on a tree trunk differs in the Mountain Chickadee from that of the Pygmy Nuthatch as shown in tracings from photographs of birds at same site. (After Frank Richardson,* Adaptive Modifications for Tree Trunk Foraging in Birds, *University of California Publications in Zoology, 46(1942):317–368.)*

The relative stance of the Diving and Dabbling Ducks, for example, can be measured through descriptions and drawings (Fig. 24·1). The adaptive nature of posture in clinging to tree trunks can be measured for birds like the Chickadee and Nuthatch (Fig. 24·1). Measurements of *living action* add to the advancement of ornithology, for they may be evaluated and compared with confidence in their exactness. The skill of the observer in the field (as in the laboratory or library also) limits ornithological research often before methods of measurement limit it. But the development of new methods of measurement goes on continuously. Field ornithology has contributed so much to the biology of living things that in their capacity to observe and measure in the field, bird students very justly may take great pride.

Role of the Avocational Scientist. It may be said with little fear of refutation that except for such sciences as chemistry and medicine, ornithology leads the scientific field in the gathering and understanding of knowledge. The reason for its position in advance of so many other sciences rests largely on its great supply of avocational scientists, coupled with the innate personal interest that draws people into bird study. A large proportion of the references and suggested reading titles in this book have been written by nonprofessionals, which testifies to the effectiveness of nonpaid, avocational scientists in ornithology. (Actually, most of the ornithology of the English-speaking world is done by "amateurs.")

For bird study, the need may be simple—a bird in the back yard, binoculars about the neck, a notebook in one hand, a pencil in the other. Bird study may involve long trips, journeys to foreign lands, remote places, rigorous climates. It may involve early rising, late retiring, odd hours, long days. It may take one afield in rain, heat, cold, wind, snow. The way may be through swamps or over tundras amidst clouds of mosquitoes; it may be through desert with hot sun, deep thirst. All this and more too, the avocational scientist calls fun—works longer, harder, more carefully at it than otherwise. For this, ornithology is the gainer and to it science owes much. The charm of birds adds measurably to the advancement of science by stimulating the study of birds.

Observational Techniques. No amount of description can tell one as much about how to observe as the actual practice of the art. Most field guides include instructions on observing (e.g., Pough, 1946), books on bird watching are available (e.g., Nicholson, 1932; Hickey, 1943; Fisher, 1951), essays on bird study may be consulted (e.g., Griscom, 1945), and textbooks contain techniques (e.g., Wing, 1951).

Direct observation requires skill in seeing things (which can be developed with practice) and care in interpreting their meaning. The latter comes with experience and knowledge, especially in knowing what others have discovered. This book, it is hoped, will help in providing some background knowledge, though it must be supplemented by practice in the field. Reading of sign needs a far more practiced skill than does direct observation. An observer of nesting, even from a blind, cannot watch events every minute from start to end of the nesting period unless he teams up with others. A nest destroyed often bears characteristic work of the destroyer. An empty nest may be vacant because eggs have hatched, have not been laid as yet, or have disappeared. Sitting in a blind watching a Cowbird remove an egg from an Ovenbird nest (e.g., Hann, 1941) is a direct method of observation. But determining from the way the eggs were eaten that a skunk did the job is an indirect method of observation through the use of interpretation.

Scientific Method. Field observation under natural (and sometimes experimental) conditions uses both direct and indirect observation to amass data for analysis. From these data by interpretation through *inductive reasoning*, scientists arrive at conclusions. The "scientific method" consists of carefully collecting facts, testing their validity the meanwhile, analyzing and interpreting the data, and drawing logical conclusions. No one should suppose for a moment that conclusions so drawn are immutable. They must always be considered as based on the material of the moment; they may be changed with time in some cases, they may not in others. Thus, when Aristotle said that large birds migrated across the Mediterranean to Africa, he stated a conclusion unchanged after twenty and more centuries. But when he repeated the idea that small birds "hitch-hiked" across on larger birds, he stated a conclusion long since rejected. The acceptance of a conclusion in any field of science varies widely. It depends upon its timeliness, adequacy of data, reputation of its author, strength of contrary opinion, and vigor of its presentation. That many papers unearth and support the neglected work of others shows how even sound scientific work may not be recognized at once for its true worth.

Conclusions often develop into *generalizations*, which vary in the degree of establishment and acceptance. Though much variation in meaning and differences of opinion make for overlapping and even use of different terms for the same general thing, scientists use such terms as *postulate*, *hypothesis*, *theory*, *rule*, *principle*, and *law* for general conclusions. Thus, the *Biogenetic Law* and *Theory of Recapitulation* mean the same generalization. The *Bergmann Rule* is sometimes called the *Bergmann Principle* or even *Bergmann Law*. Postulates, hypotheses, and theories are generalizations of a lower order of acceptance; they are temporary conclusions that may advance later to the "generally accepted" and "proved" category. But many are discarded.

EQUIPMENT FOR THE FIELD

Field Records and Notes. Bird students keep records in a variety of ways, all suited more or less to the experience and needs of the user. No one method has all the advantages and much can be said for each of the different ways in vogue. By and large, personal convenience, personal preference, and the way one started determine the method of keeping records. Most bird students keep journals of some sort into which they enter notations and observations on matters of interest. (Fortunately, bird students or their heirs tend to provide for permanent preservation in museums, libraries, and scientific archives.) Commonly, notebooks take the form of journals in literary form. A few ornithologists use small notebooks and transfer their records to a card file or other systematized record on a species basis. Others prefer a small notebook for brief notes at the moment of observation, which they later expand when transferring to the journal, generally at night. But still others carry the journal or pages from it afield and write down completely the observation at the time (which is to be preferred). A note so written leaves out less, but one written at leisure may be more exhaustive though largely left to memory. But it should be emphasized that memory is fleeting and after a few hours may be inaccurate.

Little preference need enter into selection of paper other than that it be a good permanent, rag paper. Some people prefer buff color, but white is satisfactory, for one may turn his back to the sun and thereby reduce glare. Ink tends to smear in wet weather; it may fade unless a carbon ink is used; but few carbon inks work well in most fountain pens. Soft pencils may smudge if used on both sides of a page and sometimes do so when used on one side, but dipping the page in water and drying it out reduces smudging. Hard pencils ordinarily are useable, though they may not write very black under some conditions.

Preference also determines the size of the notebook or card file. But in general, standard business sizes should be preferred. Those 8½ by 11 inches serve well but prove ungainly in the field. One-half this size (5½ x 8½) seems best, though many people prefer an intermediate size. For card files, the 3 by 5 and 4 by 6 usually serve for most purposes, but larger sizes have their uses.

Migration, nesting, and similar data lend themselves very well to record books similar to the account journals of bookkeepers. A horizontal line may be used for each species and a vertical column for each day or week. These may be used also for keeping a daily account of birds seen. In order to avoid the repeated writing of names, short sheets may be used as inserts, or one may use a large sheet nearly wall size.

For repeated observations of the same kind, prepared forms materially speed record keeping; they reduce omissions and forgetfulness also. When a number of different observers collect field data on the same kind of thing, forms materially increase efficiency afield. The working up of data later will be easier and more complete. For a series of nest observations, an observer may with profit prepare a set of forms providing a space for common entries, such as nest site, nest size, height above the ground, distance from trunk, number of eggs, band numbers given to the young, and many other items. Some observers provide for very detailed collecting of information in this manner.

Use of Maps. Maps have many uses and even the poorest draftsman can make a useful field sketch. Maps may be made by simple visual estimate from a point of vantage. But more accurate ones are made by pacing or using a plane table (Raisz, 1948). Maps may be made from aerial photographs now available in the courthouses of nearly all the settled parts of the United States and Canada. Plat maps, road maps, topographic maps, land-use maps, soil maps, and some special kinds may be found for various areas. Many such available maps will serve as a convenient base for tracing a working map; some may be used directly. A small supply of maps can be made by tracing over carbon paper, but a stationery store will run off a supply by duplication at very little cost.

Field Identification. The facility for identifying birds afield has been materially aided by the several field guides available; these describe the respective means for identifying any bird in the United States and Canada (see Suggested Reading). Similar guides for other parts of the world are a much-needed item. But no field guide will substitute for practice and no field guide will convey some of the subtle differences often used by more experienced observers. Birds clinging to a tree trunk as shown in Fig. 24·1 readily indicate *Chickadee* or *Nuthatch* to one familiar with them. Without too much difficulty, an observer in the western forests could tell fairly easily what species. The fact that the Raven has a rather hawklike flight gait readily distinguishes it from a Crow to many observers. The quick flaps and bobbed look of the Black Vulture are unlike those of the Turkey Vulture. To some, the Pelicans can be identified by their peculiar look when sailing, as though "sitting through the air." Many of these subtle marks can be described, but others must be learned by the observer himself.

Going Afield. There is no such thing as a "best time" for going afield for general bird study. Each purpose has its own time. Likewise, there is no best place, for each purpose also has its own profitable places. If one wishes to see birds at the height of activity and animation, for example, probably the best time would be in the spring shortly after sunrise. At such a time, birds will be active, the males will be singing, often on exposed perches. And no greater thrill can come to the bird watcher than the springtime with birds singing.

Where to go depends upon the birds wanted and the season of the year. An observer with a small amount of time will find many suitable places near and far, some of which have been listed for convenience (Pettingill, 1951, 1953).

Few ornithologists study birds at night, but nighttime has many attractions, though staying up without sleep is hardly one of them. The singing of nocturnal birds is definitely a subject for night study. Many Shorebirds feed at night, especially in the moonlight. Many ground birds can be caught and banded at night by headlighting and catching with clap-nets. Bird eyes usually reflect as brilliant orange-red at night, often about the color of a live coal. This eye shine can be used in night study (Van Rossem, 1927). But the exact color varies with the intensity of light and the angle of vision. Among those shining red are Killdeer, Woodcock, Barred Owl, Whip-poor-will, Nighthawk, Chuck-will's-widow, and Poor-will. Night-roosting by ground and tree birds alike is little known, and some suggestions for study have been made (Moore, 1945).

Bird students regularly keep lists, such as by trip, day, or habitat type. For convenience, some prepare printed check-list cards on which to keep records. Others prefer to write the names of birds as seen and then to enter the numbers. Printed cards have the advantage of stimulating the mind, so that fewer birds are likely to be overlooked. For increased usefulness, field record cards may include items of weather, habitat, and time. The usual ones recorded include many of the following and sometimes other ones also:

Date
Hours afield
Hour of observation
Place
Temperature
Wind and direction
Cloudiness
Humidity
Rain
Visibility
Barometer
Altitude
Cover type
Vegetation conditions

Few daily lists of more than one hundred birds can be amassed by an individual except by great effort in favored localities or during the migration season. A few dozen species is the more usual number.

A yearly list of two hundred birds in one locality is good. One hundred fifty is the more usual number for regions away from water. But some remarkable lists have been made by observers having the opportunity to travel and the initiative to get out with the birds and hunt for them. Life lists may run several times the seasonal list; it depends largely upon how much the observer travels.

Optical Instruments. The chief optical instrument used in bird study is the prism binocular (Fig. 24·2). It is to the field observer what the microscope is to the laboratory technician (and it is just as reliable). Much has been written of binoculars (especially by advertising writers) but other than for coated lenses, no significant optical improvements have been made since the turn of the century. Improvements have been chiefly mechanical, especially in the use of light alloys, as well as the perfection of coated lenses. The commonly used bird glasses are of six, seven, eight, nine, and ten powers of magnification, denoted respectively as 6X, 7X, 8X, 9X, and 10X. The objective lens determines the amount of light that enters the binocular, and the "light-gathering power" is usually given as the square of the quotient obtained by dividing the diameter of the objective lens in millimeters by the magnification. The construction of inferior binocu-

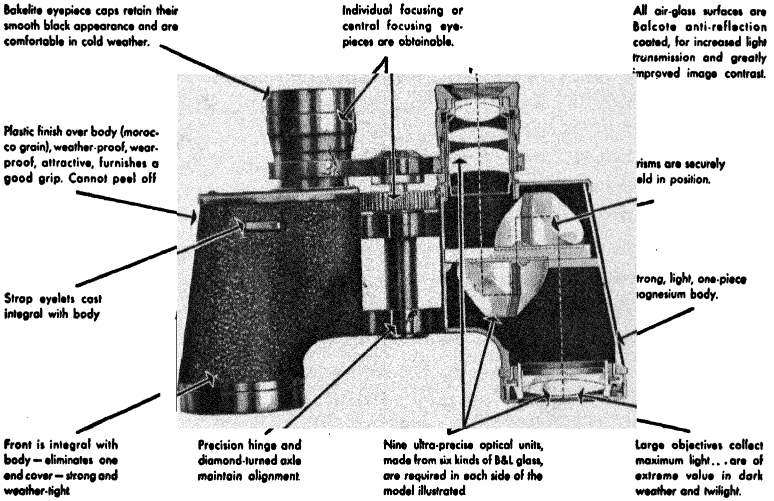
Bakelite eyepiece caps retain their smooth black appearance and are comfortable in cold weather.
Individual focusing or central focusing eyepieces are obtainable.
All air-glass surfaces are Balcote anti-reflection coated, for increased light transmission and greatly improved image contrast.
Plastic finish over body (morocco grain), weather-proof, wear-proof, attractive, furnishes a good grip. Cannot peel off
risms are securely eld in position.
Strap eyelets cast integral with body
trong, light, one-piece agnesium body.
Front is integral with body—eliminates one end cover—strong and weather-tight
Precision hinge and diamond-turned axle maintain alignment.
Nine ultra-precise optical units, made from six kinds of B&L glass, are required in each side of the model illustrated
Large objectives collect maximum light. . . are of extreme value in dark weather and twilight.

Fig. 24·2. *Cut-away view showing parts of a sturdy, well-made, wide-field prism binocular suitable for bird study. (Bausch & Lomb Optical Co.)*

lars, however, may not permit utilization of all the light entering the objective lens. A 6 × 30 glass has a light-gathering power of twenty-five as does also a 7 × 35, or an 8 × 40. No glass of less light-gathering power than twenty-five should ordinarily be purchased for bird study.

For especially clear observation in deep woods, on dull days, or at twilight, binoculars with large objective lenses are favored. The 7 × 50 is the most commonly used one of this kind, though 6 × 42, 8 × 56, and others are available and are excellent instruments. Manufacturers sometimes designate such a large objective lens binocular as a "night glass." All such glasses are heavy to carry, but their superior qualities offset this for many observers. On a clear day, however, the limit of light is in the human eye itself, and all clear binoculars of good quality are about equally suitable in sunlight.

The construction determines the field of view (not the relative size of the objective lens), so that a 6 × 30 glass may have a wider field than a 7 × 50. Manufacturers give the field as the diameter of the observation view at 1,000 yards. (In order to be more impressive, advertising writers prefer to specify this distance in feet rather than yards, e.g., 450 feet at 1,000 yards instead of 150 yards at 1,000 yards.) Wide-field binoculars have an extra lens, and are rather more expensive than regular binoculars. Since so much depends upon field of view for rapidly locating birds, one should get as wide a field as possible. Because the field decreases with increase in magnification (unless constructed to compensate for this), low-power binoculars are easier to use in locating an object. They also may be held more steadily in the hand. The usual regular binocular has a field of view of about 330 feet in the 8× and about 450 in the 6×. A wide-field 8× will have a field of about 450 feet.

Center focusing and individual focusing eyepieces have their respective advantages and followers. For hard and long service, the sturdiness of the individual focusing should dictate its choice. With experience, it may be focused with about the same rapidity as the center focusing type. In practice, the observer focuses on some distant object (which gives him "infinity" as in a camera) and notes or marks the reading on the barrel scales. For fully three-quarters of his observations, the average ornithologist need make no further adjustments, for his eyes can do it for him. For closer objects, one adjusts the eyepieces. By a glance at the barrel scales, the binoculars may be returned to the "infinity" (hence, "fixed focus") position, which constitutes the "ready" position for him.

Because so many binoculars of inferior quality (mostly imported) have flooded the market, the bird student should tread warily in purchasing any binoculars other than those made by one of the standard, long-time manufacturers (Reichert and Reichert, 1951). For used glasses of any make and new glasses of any except the few time-tested ones, the bird student should depend upon *competent* advice (a rarity) before purchase. Surplus glasses of the *American* army or navy (even of World War I) are optically and structurally well made, though the condition of wear may render them unsuitable for purchase. Even so, many glasses are not suitable or convenient for bird study, though they may be sound instruments nevertheless. Few dealers in the field are competent to advise on the matters of binoculars, and the prospective purchaser of binoculars is well advised to seek the recommendations of qualified ornithologists.

Spotting scopes are useful in the study of Waterfowl, birds in mountains, and for many other special purposes. A few binoculars of great magnification (16× to 24×) have been manufactured that are exceptional instruments for special studies with a tripod. They may be used in nesting studies, for example, at enough distance from the nest to omit a blind. Spotting scopes and telescopes have been sighted against the moon for migration studies. Radar has been tried in flock studies. Infrared spotting devices have been tried for night work. A mirror on a rod serves as an instrument for examining nests out of reach.

Visual Distance. The distance at which a bird may be recognized varies with observers and conditions of observation. For practice in estimating distance, cutouts or wooden models may be perched or suspended by threads at known distances. Some measure of the visual distance in feet for good eyesight has been reported (Table 24·1).

Table 24·1

Visual Distance for Good Eyesight

Species	Visual Distance
Hummingbird	100 ft., on wire
Swallow	250 ft., on wire
American Goldfinch	200 ft., flying
American Robin	250 ft., identified by shape 500 ft., shows as a dot 750 ft., noticed only by the best of eyes
American Crow	Can be seen twice the distance of the American Robin
Broad-winged Hawk	Recognized as Hawk at one-half mile
Turkey Vulture	4,700 ft., recognized as a soaring bird

Source: Harold B. Wood, "How Far Can a Bird Be Seen?" *Auk,* 54(1937):96–97.

Photography. No particular "tricks" are necessary for most bird photography other than skill, patience, and care. For good work, a suitable camera is essential, but for an occasional picture now and then, many common cameras are useable. Color photographs are often taken in 35mm. size because of convenience and expense, but larger sizes take better pictures. Many people use miniature black and white cameras with success, but no small camera can take the quality picture produced by larger cameras, except under fortunate circumstances. Reflex cameras, particularly the *Graflex* with extension bellows, take the largest proportion of prize winning pictures. Telephoto lenses and extension bellows are essential additions to the equipment of a bird photographer.

A small, compact camera with an extension bellows proves to be the most versatile, though not so handy as a miniature camera nor so likely as the *Graflex* to take superior pictures. Yet anyone who plans to take pictures in the field must expect to put some effort and care into each picture. Success in bird photography seldom comes by taking snapshots; effort pays off. The camera has many uses in bird study, such as the study of action, posture, behavior. (Fig. 24·1b shows an example of the study of clinging by tree-trunk birds by means of a camera set to take pictures at the same spot; the outline of the birds has been drawn from the photographs.) The taking of flight pictures by high speed photography has been especially successful and offers opportunities for further study (see Fig. 15·7).

Motion pictures in color have an important role in instructing people in bird life. Since the lives of birds are most entertaining subjects for pictures, skillfully edited motion-picture photography of birds in color can hardly become an exhausted art in the foreseeable future. Motion pictures have been used successfully in the study of motion and behavior, but color film may not be needed. In general, all the precautions, problems, and skills of still photography apply with equal or greater force to motion-picture photography of birds.

Use of Blinds. Blinds may be built of almost any material available—roofing paper, boards, canvas, and even cornstalks (Fig. 24·3). Some photographers and ornithologists use portable blinds. Blinds may be placed in trees, on floats, or on towers; they may be in the open, in the brush, or in the woods. Birds soon learn to ignore a blind, even though it may be only a few feet from a nest. Often the blind is built some distance from the object and moved closer each day until it is in final position. Holes in the sides give openings for cameras and for watching. In general, blinds may be used at any season of the year, and they may be of any size that is easy to build. Larger ones are more comfortable, which comfort increases the observer's efficiency.

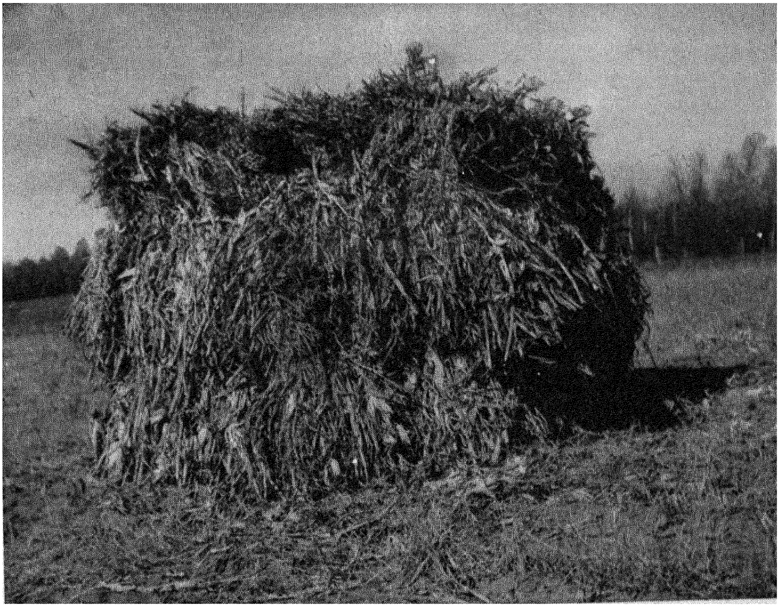

Fig. 24·3. *Cornstalk blind built to photograph and study Prairie Chickens at a winter feeding area. (Photograph by Leonard W. Wing.)*

Recording Instruments. Many normal laboratory and weather instruments such as the kymograph, thermograph, barograph, hygrograph, and anemometer have long been used in bird study. A number of special devices have been developed, and ingenious ornithologists yearly develop more. An activity recorder consisting of a drum turned by a clockwork, a roll of adding machine tape, a recording pencil, and nest contacts will keep a record of the coming and going at a nest box or at an open nest. Any ornithologist of modest mechanical ability can construct one.* More complicated instruments are the recording potentiometers that use thermocouples.† The development of radioactive trace elements and Geiger counters gives a new tool for field and laboratory use in bird study, though perhaps a dangerous one.

Sound recording instruments have made it possible to bring bird sound into the laboratory for analysis on sound tracks (Brand, 1938) or recording tape. The latter may be used with an audiospectrograph for converting the sound to marks on paper (Borror and Reese, 1953). Many phonograph records of bird song provide opportunity to hear a great many songs whenever one wishes (e.g., the famous Cornell bird-song records).

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* Useable illustrations or descriptions will be found in *Auk*, 47(1930):471–480; *Bird-Banding*, 4(1933):33–40; *Wilson Bulletin*, 49(1937):145–237.

† *Auk*, 44(1927):206–216; 47(1930):471–480.

FIELD TECHNIQUES

Relative and Absolute Abundance. Two general ways of measuring numbers, absolute and relative abundance, are open to the field observer, but relative abundance is the more commonly used in actual practice. Adjectival indicators of relative abundance have long been used, though the reader must have some knowledge of conditions before evaluating such descriptive terms. Yet their use always has had a place in bird study and doubtless always will. A graded series of adjectives would be: rare, uncommon, common, and abundant. Another series might be: rare, scattered, frequent, common, and abundant.

Relative abundance, as the term implies, measures numbers or distribution relative to some other factor. Two common measurements are by relative numbers and relative frequency-of-occurrence. The former is commonly called merely "relative abundance," which is a little confusing. A bird observed in 3 out of 10 days afield could be given a rating of 0.3 as its frequency-of-occurrence. Three individuals counted in 10 hours afield would have a relative number of 0.3 birds-per-hour. If the observer traveled 10 miles, it would be 0.3 birds-per-mile. The frequency-of-occurrence has been employed with success many times (e.g., Linsdale, 1936b). Other data obtained from time to time have been Hawks seen while an observer travels, flock counts, singing birds, nest counts, brood counts, and many others. A note pad in the car is a handy place to record birds or flocks seen while traveling.

Attempts to obtain more quantitative data, particularly those which can be used statistically or for population estimates, have been numerous. Strip counts, based chiefly upon distances of detection, have been used with varying results. The *detection distance* represents the distance from the observer to the bird at the moment of its discovery (a *flushing distance* is one kind). From these distances is computed the number of birds in a strip along each side of the travel route by using the average detection distance, preferably computed separately for each group of distances (Hayne, 1949). The figure thus obtained becomes a sample estimate for determining total population. In the field, noting the cover type in bird counts is but the work of a moment; yet it is likely to increase greatly the usefulness of the records.

Absolute abundance reports the number of birds in a specified area, usually as sample counts. Because of the inherent difficulty in making them, few absolute counts other than on sample areas have been made.

Sample Areas. Sample areas, often called *quadrats* or *sample plots,* may be used as census areas in bird study. They may or may not be confined to a single vegetation type. To be a sample, however, an area should actually represent the thing being sampled. This seems rather simple, but the practical difficulties in finding a sample area and in determining its relative merits are often formidable. The breeding-bird censuses sponsored by *Audubon Field Notes* are the census-plot type of sample area. Many state game departments and others have sample areas where birds and other animals (as well as vegetation) may be counted from time to time.

Sample areas may be permanent plots having carefully established lines and markers for successive visits. They may also be temporarily established areas for a single season or even a single trip. They may be of any form to fit topographic or vegetational features; they may be square, rectangular, or of any other shape. The size depends upon the use and the manpower available, as well as the features of the area itself. Obviously, the larger the area, perhaps the better the count may be, but circumstances may not give an ideal situation. A count of the bird life of the virgin vegetation of a prairie region might have available only a few acres of relict grassland.

Transects are lines, at random or by pattern (replicated), through the vegetation and area to be surveyed. They may be set as compass lines. In a sense, they are *extended quadrats,* the width of which has been reduced to a line.

Bird Bandings. The first bird banding (called "ringing" in Europe), like so many other important scientific events, occurred in early times—it was done long ago by someone interested in birds. It is written that in Germany, a Common Heron captured in 1710 carried leg bands ("several metal rings"), one apparently attached in Turkey. John James Audubon thus marked a brood of Eastern Phoebes in 1803 (Pennsylvania). European use of bands began somewhat systematically in 1899 (Holland) when H. C. C. Mortensen banded White Storks, European Teals, and Starlings. It began systematically in America in 1902 when Leon J. Cole reported upon it and when Paul Bartsch banded 101 nestling Black-crowned Night Herons with bands marked "Return to Smithsonian Institution." Bands marked "Notify Auk, N. Y., Box Z, Yale Station, New Haven, Conn.," and various other legends were used independently and under auspices of the American Bird Banding Association and its predecessors. Early in 1920, the former Bureau of Biological Survey undertook sponsorship, which has been continued under its successor. Through fortunate cooperation between Canada and the United States, all banders do uniform banding with the same bands, except for the banding of Pheasants and a few other nonmobile game species.

Interested banding cooperators do most of the banding. They may have banding stations for capturing adults or they may band young, as at nesting colonies. Many Waterfowl refuges band Waterfowl, often in large numbers. Though a higher percentage of returns comes from the banding of adults, more complete data (hence more valuable) come from the banding of young birds, which act fixes both the age and place of hatching.

Trapping for Banding. A very ingenious series of traps has been developed for banding birds (Lincoln, 1947). Birds that feed upon grains, such as the Cowbird, Grackle, Waterfowl, and Finches, come readily to baited ground traps, either automatic or tripped by an attendant. Large numbers, often several dozen at a time, may be caught. Nets have been used with success, both "mist" nets and nets thrown by elastic bands or "cannons."

Tree-trunk traps catch tree-climbing birds by means of a lead-in around the tree to direct the birds into the trap openings. Traps placed atop chimneys have captured a large number of Chimney Swifts. Warblers have been found to decoy readily to water in motion, an attraction created in a trap by use of dripping water. Nesting birds can be caught by traps over nests. In actual practice, most species have been caught in some sort of trap, though efficient ones for catching many species have not been perfected. General traps follow several patterns built around the principle of deception by which the entrapped birds cannot find the entrance or with doors shut after the birds have entered. Specialized traps vary widely in design and type of attraction used.*

Colored Bands. Just as it can be said that banding has greatly advanced bird study, so also can the techniques of marking birds for individual identification afield be termed of the very greatest importance in many kinds of field studies. Though banding marks the bird as an individual, it must be recaptured in order to read the band number. Bands with printed numbers have been used and can be read at some distance with binoculars, but such numbers must be very large, as must also the bird carrying the band. Colored bands in combination with aluminum bands (Fig. 24·4) have long been used for marking individual birds (Mangels, 1938). Important cooperative studies of Gulls have been carried on with them, Gulls being especially good subjects for such study. They may be banded at nest colonies and band color combinations can be recognized at docks, on boats, and on shore.

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* *Bird-Banding*, a quarterly devoted to the subject, often publishes descriptions of new and novel traps. The circulars of the bird-banding associations (Northeastern, Eastern, Inland, and Western) also contain many suggestions for traps.

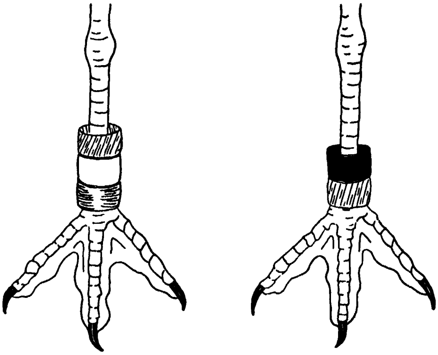

Fig. 24·4. *Colored bands, usually of plastic, in combination with aluminum bands serve as a code for individually distinguishing birds in the wild. (For purposes of illustration, the bands have been drawn larger than would be correct practice in actual banding.)*

Marking of Birds. The addition of colored feathers for marking birds has proved advantageous for short-time studies, for the added feather will remain until the next molt (A. M. Baumgartner, 1938). Plastic and other markers have been used in a similar manner. Dyeing a bird, either partly or completely, has its uses (Wadkins, 1948). A passerby seeing a peculiarly colored dead bird has been known to report bands not otherwise noticed. Birds have been marked experimentally in the field by squirting dyes under high pressure from a cylinder. Marking birds with paint or airplane dopes and lacquers has worked well, in some cases persisting for several months (Fig. 24·5). Colors have also been daubed on nests and roosts to mark the birds using them. Wing and tail feathers have been clipped to call attention to the bird.

All markers in the field must be recognizable, long-lasting, harmless to the bird, easy to apply, and in sufficient variety to distinguish the needed number of birds. Thus, four colors singly could be used to mark groups or as place markers, but if used in combination, they can be used to mark many birds individually.

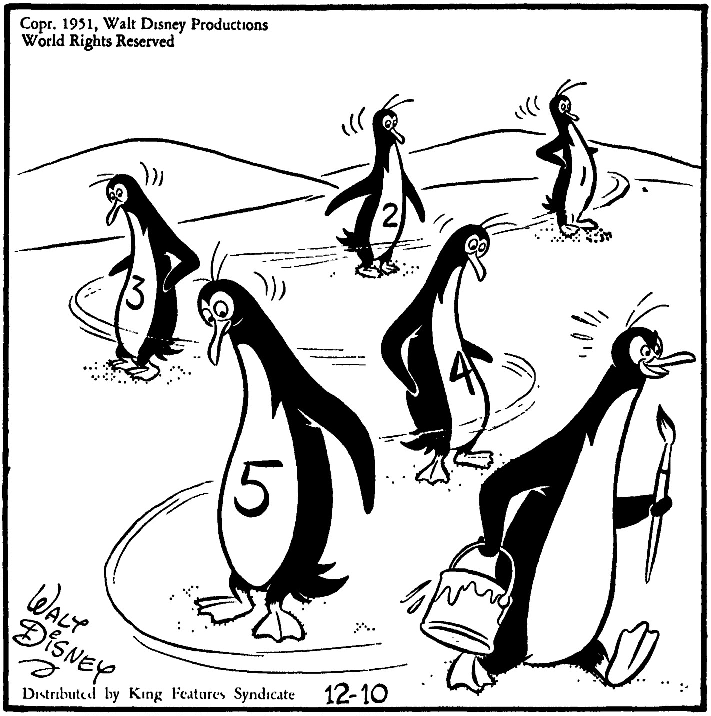
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Fig. 24·5. *"Now, by golly, I'll know who's who around this place!" That the problem of marking birds for individual recognition interests the cartoon arts evidences further the appeal of birds. (By permission from* Merry Menagerie. *Copyright, 1951, by Walt Disney Productions, Burbank Calif.)*

KINDS OF STUDIES

Ecologic Field Studies. Because birds depend upon vegetation for food and cover, any significant change in plant life reverberates through the bird life present (see Chapters 10, 11, 12). The succession of bird life in any area is no less real than that of plants, but of this little has been studied except with some game birds. Careful counts and observations of bird life in changing environment year after year reveal the succession in bird life, just as they do in plant life. But observations must be accompanied by comparable studies of the plant life and plant succession. This phase of bird work is one of promise. In addition to such year-to-year succession, a seasonal succession occurs as birds shift about with the seasons.

Studies of the relation of daily activity to weather are usually carried on by following selected species or groups of individuals and measuring carefully their daily habits and the variations brought about by weather. Around-the-clock observations, particularly in the long hours of high latitudes, are necessary for such studies.

The bird influences its plant habitat in many ways, such as by feeding upon insects, by eating the vegetation, by transporting seeds, and by droppings. Competition with other animal life doubtlessly influences the ecological relationship of which birds form a part. The influence of the bird upon the environment is far less known than that of the environment upon the bird, but they intertwine with each other.

Life History Studies. Studies of life history in ornithology have become rather more systematized than formerly. A number of excellent life-history studies give many field techniques (e.g., Stoddard, 1931; Hann, 1937; Nice, 1937, 1943; Walkinshaw, 1938; Blanchard, 1941; Lack, 1946). Books on bird watching also give attention to such matters, even in the form of suggested outlines for life histories. It seems best to refer the reader to such sources, so varied are the possible procedures. But in general, a life history study follows the species throughout the year, from egg laying to egg laying, from its summer home to its winter range and back. But seasonal life history studies have an important place and should be undertaken when longer ones cannot.

Field Studies of Migration. Because migrations (Chapter 16) is seasonal in nature, it would seem as though its study might be compressed into a few weeks afield spring and fall. For one who wishes only to list migrants in the height of the season at one place, this is true. But migration in some aspect goes on almost throughout the entire year, even at one place. Birds assemble in midsummer into flocks as a prelude to fall migration, often congregating in favored habitat. At the same time, some birds may be making postbreeding season wanderings (e.g., young Bald Eagles, Fig. 16·6). Stragglers of various species may remain behind after the main migration has moved northward, while some advance guards among the Shorebirds may be already returning.

Local wanderings of birds have long been known, but little system in such wanderings has been determined as yet. In dry regions, for example, the movement of birds to oases, river valleys, and the like, has been reported many times. Marsh birds often concentrate in favored marshes. Even birds of the forest show local movements. Just how this merges into fall migration or movements to winter quarters is largely unknown.

Field Experiments. Observation as a method of field ornithology, whether of a common bird, local avifauna, or distant bird life, has no actual limits except the time, ingenuity, and perseverance of the individual. Obviously, many of the accomplished results bearing upon a common dooryard bird apply in varying degrees to every species of bird, near or far. They may also apply in varying degrees to the same species regionally or throughout its range. How they may apply will be known only by testing for each bird in each area.

Birds afield serve as subjects of great promise for experimental study, especially of population problems, behavior studies, and ecological relations. Many techniques have been tried, all designed to provide controls for testing the physical, social, and internal environment (Emlen, 1950). These have involved diverse things. Color discrimination, for example, has been tested by offering colored food or colored nesting material (page 364). Food preferences have been examined by offering multiple choices of foods and then studying the differences in amounts taken. Water needs and uses have likewise been examined. Even the question of sense of smell in the Turkey Vulture has been tested by exposing meat under various conditions. The territorial behavior of birds has been put to trial by moving the nest of a bird into or through the established territory of another and watching the reactions of the various birds involved. Ornithologists have added and removed eggs from nests and have observed the resulting events. Many birds have been moved from their homes to distant places to study their homing behavior, sometimes followed by an observer in an airplane. The reaction of birds in the wild to sex hormone injections has given some suggestions of the relationship between bird behavior and bird physiology. The pioneer study of day length and the sex cycle used Crows exposed to increasing day lengths before release in the wild and subsequent reports of their movements obtained from the public; for some birds, the reports were far north of the release point (Edmonton, Alberta) in mid-winter (Rowan, 1931).

Areas of vegetation denudation and change have been examined to see what influence may have been exerted on bird life, occasionally by experimental cutting and burning. The reactions of birds to removal of any potential enemies have been watched. Systematic removal of portions of the bird life itself has tested the reservoir of unmated birds and the infiltration of birds into vacant territory. It has also tested the importance of the niche as a control of bird populations and pair distribution.

SUGGESTED READING

American Ornithologists' Union, *Fifty Years' Progress of American Ornithology, 1883–1933.* Lancaster, Pa.: American Ornithologists' Union, 1933.

*Baker, John H. (ed.), *The Audubon Guide to Attracting Birds.* Garden City, N. Y.: Doubleday & Co., Inc., 1941.

Emlen, John T., *Techniques for Observing Bird Behavior Under Natural Conditions.* Annals of the New York Academy of Science, 51(1950):1103-1112.

*Fisher, James, *Watching Birds.* Harmondsworth, England: Penguin Books, Ltd., 1951.

*Griscom, Ludlow, *Modern Bird Study.* Cambridge, Mass.: Harvard University Press, 1945.

Headstrom, Richard, *Birds' Nests: A Field Guide.* New York: Ives Washburn, Inc., 1949.

*Hickey, Joseph J., *A Guide to Bird Watching.* New York: Oxford University Press, 1943.

Kendeigh, S. Charles, *Measurement of Bird Populations.* Ecological Monographs, 14(1944): 67–106.

*Morris, Perry A., *Nature Photography Around the Year.* New York: Appleton-Century-Crofts, Inc., 1938.

*Nicholson, E. M., *The Art of Bird Watching.* New York: Charles Scribner's Sons, 1932.

*Peterson, Roger Tory, *A Field Guide to Western Birds.* Boston: Houghton Mifflin Co., 1941

*Peterson, Roger Tory, *A Field Guide to Birds.* Boston: Houghton Mifflin Co., 1947.

*Peterson, Roger Tory, Guy Montfort, and P. A. D. Hollom, *A Field Guide to Birds of Britain and Europe.* Boston: Houghton Mifflin Co., 1954.

*Pettingill, Olin Sewall, Jr., *A Guide to Bird Finding East of the Mississippi.* New York: Oxford University Press, 1951.

*Pettingill, Olin Sewall, Jr., *A Guide to Bird Finding West of the Mississippi.* New York: Oxford University Press, 1953.

*Pettingill, Olin Sewall, Jr., *A Laboratory and Field Manual of Ornithology.* Minneapolis, Minn.: Burgess Publishing Co., 1956.

*Pough, Richard H., *Audubon Bird Guide (Land Birds).* Garden City, N. Y.: Doubleday & Co., Inc., 1946.

*Pough, Richard H., *Audubon Bird Guide (Water Birds).* Garden City, N. Y.: Doubleday & Co., Inc., 1951.

*Reichert, Robert J., and Elsa Reichert, "Know Your Binoculars," *Audubon Magazine,* 53(1951): 45–50, 104–109.

Wetmore, Alexander, "A Method for Keeping Notes and Files Dealing with Ornithology," *Condor,* 29(1927):109–111.

*Wing, Leonard W., *Practice of Wildlife Conservation.* New York: John Wiley & Sons, Inc., 1951.

Appendix I

References

ALDRICH, JOHN W. 1943. "Relationships of the Canada Jays in the Northwest," *Wilson Bulletin*, 56:217–222.

ALEXANDER, W. B. 1950. "The Index of Heron Population, 1950," *British Birds*, 43:78–80.

ALLARD, H. A. 1930. "The First Morning Song of Some Birds of Washington, D. C.: Its Relation to Light," *American Naturalist*, 64:436–469.

ALLEE, W. C. 1942. "Group Organization Among Vertebrates," *Science*, 95: 289–293.

———. 1951. *Cooperation Among Animals.* Henry Schuman, Inc., New York.

ALLEE, W. C., ALFRED E. EMERSON, ORLANDO PARK, THOMAS PARK, and KARL P. SCHMIDT. 1949. *Principles of Animal Ecology.* W. B. Saunders Co., Philadelphia.

ALLEN, ARTHUR A. 1914. "The Red-winged Blackbird: A Study in the Ecology of a Cat-tail Marsh," *Abstract of the Proceedings of the Linnean Society of New York, 1911–1913.*

———. 1930. *The Book of Bird Life.* D. Van Nostrand Co., Inc., New York.

ALLEN, FRANCIS H. 1939. "Effect of Wind on Flight Speeds," *Auk*, 56:291–303.

ALLEN, GLOVER M. 1925. *Birds and Their Attributes.* Marshall Jones Co., Francestown, N. H.

ALLEN, ROBERT P. 1942. *The Roseate Spoonbill.* National Audubon Society, Research Report No. 2.

———. 1947. *The Flame Bird.* Dodd, Mead & Co., Inc., New York.

———. 1952. *The Whooping Crane.* National Audubon Society, Research Report No. 4.

AMADON, DEAN. 1943a. "Bird Weights as an Aid in Taxonomy," *Wilson Bulletin*, 55:164–177.

———. 1943b. "Bird Weights and Egg Weights," *Auk*, 60:221–234.

———. 1947a. "Ecology and the Evolution of Some Hawaiian Birds," *Evolution*, 1:63–68.

———. 1947b. "An Estimated Weight of the Largest Known Bird," *Condor*, 49:159–164.

———. 1953. "Migratory Birds of Relict Distribution: Some Inferences," *Auk*, 70:461–469.

AMERICAN ORNITHOLOGISTS' UNION. 1953. *Fifty Years' Progress of American Ornithology, 1883–1933.* Lancaster, Pa.

ARMSTRONG, EDWARD A. 1947. *Bird Display and Behavior.* Lindsay Drummond, Ltd., London.

———. 1949. "Diversionary Display," *Ibis,* 91:88–97, 179–188.

———. 1950. *Bird Life.* Oxford University Press, New York.

AUBER, L., and MURIEL Y. MASON. 1955. "Structurally Coloured Pattern Marks on the Inner Web of Flight Feathers," *Ibis,* 97:259–265.

AUSTIN, OLIVER L. 1945. "The Role of Longevity in Successful Breeding by the Common Tern (*Sterna hirundo*)," *Bird-Banding,* 16:21–28.

———. 1948. "Predation by the Common Rat (*Rattus norvegicus*) in the Cape Cod Colonies of Nesting Terns," *Bird-Banding,* 19:60–65.

———. 1949. "Site Tenacity: A Behavior Trait of Common Tern (*Sterna hirundo* Linn)," *Bird-Banding,* 20:1–39.

AVERILL, CHARLES K. 1923. "Form of Egg and Extent of Migration," *Condor,* 25:163–165.

AYMAR, GORDON C. 1935. *Bird Flight.* Dodd, Mead & Co., Inc., New York.

BAERG, W. J. 1930. "The Song Period of Northwest Arkansas," *Auk,* 47:32–40.

BAHR, P. H. 1907. "On the 'Bleating' or 'Drumming' of the Snipe (*Gallinago coelestis*)," *Proceedings of the Zoological Society of London,* pp. 12–35.

BAILEY, R. WAYNE, HANS G. UHLIG, and GEORGE BREIDING. 1948. *Wild Turkey Management in West Virginia.* Conservation Commission of West Virginia, Game Management Bulletin No. 2.

BAKER, E. C. STUART. 1942. *Cuckoo Problems.* H. F. & G. Witherby, Ltd., London.

BAKER, FREDERICK S. 1944. "Mountain Climates of the Western United States," *Ecological Monographs,* 14:223–254.

BAKER, JOHN H. (ed.). 1941. *The Audubon Guide to Attracting Birds.* Doubleday & Co., Inc., New York.

BALDWIN, PAUL H. 1947. "The Life History of the Laysan Rail," *Condor,* 49:14–21.

BALDWIN, S. PRENTISS, and S. CHARLES KENDEIGH. 1932. *Physiology of the Temperature of Birds.* Science Publications, Cleveland Museum of Natural History, No. 3.

———. 1938. "Variations in Weight of Birds," *Auk,* 55:416–467.

BARLEY, ROBERT E. 1952. "The Incubation Patch of Passerine Birds," *Condor,* 54:121–136.

BARTSCH, PAUL, W. H. BALL, W. ROSENZWEIG, and S. SALMAN. 1937. "Size of Red Blood Corpuscles and Their Nucleus in North American Birds," *Auk,* 54:516–519.

BAUMGARTNER, A. MARGUERITE. 1938. "Experiments in Feather Marking Eastern Tree Sparrows for Territory Studies," *Bird-Banding,* 9:124–135.

BAUMGARTNER, FREDERICK M. 1938. "Courtship and Nesting of the Great Horned Owls," *Wilson Bulletin,* 50:274–285.

BEACH, FRANK. 1948. *Hormones and Behavior.* Paul B. Hoeber, Inc., New York.

BEARD, DAN (ed.). 1942. *Fading Trails.* The Macmillan Co., New York.

BEDDARD, FRANK E. 1898. *The Structure and Classification of Birds.* Longmans, Green & Co., New York.

BEDICHECK, ROY. 1950. *Karankaway Country.* Doubleday & Co., Inc., New York.

BEEBE, C. W. 1915. "The Tetrapteryx Stage in the Ancestry of Birds," *Zoologica,* 2:39–52.

BEECHER, WILLIAM J. 1951a. "A Possible Navigation Sense in the Ear of Birds," *American Midland-Naturalist*, 46:367–384.

———. 1951b. "Adaptation for Food Gathering in the American Blackbirds," *Auk*, 68:411–446.

BEISTER, H. E., and L. H. SCHWARTZ (eds.). 1948. *Diseases of Poultry*. Iowa State College Press, Ames, Iowa.

BENT, ARTHUR CLEVELAND. 1919—. *Life Histories of North American Birds*. Bulletins, United States National Museum.

BERRY, EDWARD W. 1930. *The Past Climate of the North Polar Region*. Smithsonian Miscellaneous Collections, 82: No. 6.

BISSONETTE, THOMAS HUME. 1937. "Photoperiodicity in Birds," *Wilson Bulletin*, 49:241–270.

———. 1938. "Experimental Control of Sexual Photo-Periodicity in Animals and Possible Application to Wild-Life Management," *Journal of Wildlife Management*, 2:104–118.

BLAKE, CHARLES H. 1947. "Wing Flapping Rates of Birds," *Auk*, 64:619–620.

———. 1948. "The Flight of Swallows," *Auk*, 65:54–62.

BLANCHARD, BARBARA D. 1941. "The White-crowned Sparrows (*Zonotrichia leucophrys*) of the Pacific Seaboard: Environment and Annual Cycle," *University of California, Publications in Zoology*, 46:1–178.

BOYD, ELIZABETH M. 1951. "The External Parasites of Birds: A Review," *Wilson Bulletin*, 63:363–369.

BRADLEY, O. C., and TOM GRAHAME. 1950. *Structure of the Fowl*. Oliver & Boyd, Edinburgh.

BRAND, ALBERT R. 1938. "Vibration Frequencies of Passerine Bird Song," *Auk*, 55:263–268.

BRAY, CHARLES W., and W. H. THURLOW. 1942. "Temporary Deafness in Birds," *Auk*, 59:379–387.

BRECKENRIDGE, W. J. 1956. "Measurements of the Habitat Niche of the Least Flycatcher," *Wilson Bulletin*, 68:47–51.

BRODY, SAMUEL. 1945. *Bioenergetics and Growth*. Reinhold Publishing Corp., New York.

BROLEY, CHARLES L. 1947. "Migration and Nesting of Florida Bald Eagles," *Wilson Bulletin*, 59:3–20.

BROOKS, MAURICE. 1942. "Birds at the Extremities of Their Ranges," *Wilson Bulletin*, 54:12–16.

BROWN, C. EMERSON. 1928. "Longevity of Birds in Captivity," *Auk*, 45:345–348.

BULLOUGH, W. S. 1951. *Vertebrate Sexual Cycles*. Methuen & Co., Ltd., London.

BUMPUS, HERMON C. 1899. "The Elimination of the Unfit as Illustrated by the Introduced Sparrows, *Passer domesticus*," *Biological Lectures of the Marine Biological Laboratory*, Woods Hole, Mass.

BUSS, IRVEN O. 1942. "A Managed Cliff Swallow Colony in Southern Wisconsin," *Wilson Bulletin*, 54:153–161.

CARDINELL, H. A., and D. W. HAYNE. 1945. *Corn Injury by Red-Wings in Michigan*. Michigan Agricultural Experiment Station, Technical Bulletin No. 198.

CARSON, RACHEL L. 1950. *The Sea Around Us*. Oxford University Press, New York.

CHANCE, EDGAR P. 1940. *The Truth About the Cuckoo.* Country Life, Ltd., London.

CHANCE, EDGAR P., and HARRY W. HANN. 1942. "The European Cuckoo and the Cowbird," *Bird-Banding*, 13:99–103.

CHANDLER, ASA C. 1916. "A Study of the Structure of Feathers, with Reference to Their Taxonomic Value," *University of California, Publications in Zoology*, 13:243–446.

———. 1949. *Introduction to Parasitology.* John Wiley & Sons, Inc., New York.

CHAPIN, JAMES P. 1954. "The Calendar of Wideawake Fair," *Auk*, 71:1–15.

CHENEY, SIMEON PEASE. 1891. *Wood Notes Wild, Notations of Bird Music.* Lee & Shepard, Boston.

CHITTY, DENNIS. 1938. "A Laboratory Study of Pellet Formation in the Short-eared Owl (*Asio flammeus*)," *Proceedings of the Zoological Society of London*, 108:267–287.

CLARKE, WILLIAM EAGLE. 1912. *Studies in Bird Migration.* 2 vols. Gurney & Jackson, London.

CLEMENTS, FREDERIC E., and VICTOR E. SHELFORD. 1939. *Bio-ecology.* John Wiley & Sons, Inc., New York.

COLE, LEON J. 1930. "A Triple Allelomorph in Doves and Its Interspecific Transfer," *Anatomical Record*, 47:389.

COLE, LEON J., and WILLIAM F. KIRKPATRICK. 1915. *Sex Ratios in Pigeons, Together with Observations on the Laying, Incubation, and Hatching of Eggs.* Rhode Island Agricultural Experiment Station, Bulletin No. 162.

COLE, LEON J., HERBERT L. STODDARD, and E. V. KOMAREK. 1949. "Red Bobwhite: A Report and Correction," *Auk*, 66:28–35.

COLLIAS, NICHOLAS E., and RICHARD D. TABER. 1951. "A Field Study of Some Grouping and Dominance Relations in Ring-necked Pheasants," *Condor*, 53:265–275.

COOKE, MAY THACHER. 1937. *Flight-Speeds of Birds.* United States Department of Agriculture, Circular No. 428.

COOMBES, ROBERT A. H. 1950. "The Moult Migration of the Sheld-duck," *Ibis*, 92:405–418.

COTT, HUGH B. 1952. "The Palatability of the Eggs of Birds," *Proceedings of the Zoological Society of London*, 122:1–54.

———. 1953. "The Exploitation of Wild Birds for Their Eggs," *Ibis*, 95:409–449, 643–675.

COTTAM, CLARENCE, CECIL S. WILLIAMS, and CLARENCE A. SOOTER. 1942. "Flight and Running Speeds of Birds," *Wilson Bulletin*, 54:121–131.

COUES, ELLIOTT. 1903. *Key to North American Birds.* Dana Estes Co., Boston.

COWLES, RAYMOND B., and WILLIAM R. DAWSON. 1951. "A Cooling Mechanism of the Texas Nighthawk," *Condor*, 53:19–22.

CRAIG, WALLACE. 1943. *The Twilight Song of the Wood Pewee* Myiochanes virens Linnaeus: *A Study of Bird Music.* New York State Museum, Bulletin No. 334.

CROWELL, ETHEL M., and SEARS CROWELL. 1946. "The Displacement of Terns by Herring Gulls at Weepecket Islands," *Bird-Banding*, 17:1–10.

CUMLEY, RUSSELL W., and LEON J. COLE. 1942. "Differentiation of Old and New World Species of the Genus *Columba*," *American Naturalist*, 76: 570–581.

DARLING, F. FRASER. 1938. *Bird Flocks and the Breeding Cycle.* Cambridge University Press, London.

DAUBENMIRE, R. F. 1946. "The Life Zone Problem in the Northern Intermountain Region," *Northwest Science,* 20:28–38.

DAVIS, DAVID E. 1950. "The Growth of Starling, *Sturnus vulgaris,* Populations," *Auk,* 67:460–465.

———. 1955. "Determinate Laying in Barn Swallows and Black-billed Magpies," *Condor,* 57:81–87.

DAVIS, MALCOLM. 1947. "Albinism in a Flock of English Sparrows," *Auk,* 64:628–629.

DEAKIN, ALAN. 1938. "Natural Hybridization and Genetics of Flickers (*Colaptes*)," *American Naturalist,* 70:585–590.

DEBEER, G. R. (ed.). 1938. *Evolution—Essays on Aspects of Evolutionary Biology.* Clarendon Press, London.

DEEVEY, EDWARD S. 1947. "Life Tables for Natural Populations of Animals," *Quarterly Review of Biology,* 22:283–314.

DELACOUR, JEAN, and ERNST MAYR. 1945. "The Family Anatidae," *Wilson Bulletin,* 57:3–55.

DEUSING, MURL. 1939. "The Herring Gulls of Hat Island, Wisconsin," *Wilson Bulletin,* 51:170–175.

DEWAR, JOHN M. 1924. *The Bird as a Diver.* H. F. & G. Witherby, London

DICE, LEE R. 1943. *Biotic Provinces of North America.* University of Michigan Press, Ann Arbor, Mich.

———. 1945a. "Measures of the Amount of Ecologic Association Between Species," *Ecology,* 26:297–302.

———. 1945b. "Minimum Intensities of Illumination Under Which Owls Find Dead Prey by Sight," *American Naturalist,* 70:385–416.

———. 1947. *Effectiveness of Selection by Owls of Deermice* (Peromyscus maniculatus) *Which Contrast in Color with Their Background.* Contributions from the Laboratory of Vertebrate Biology, University of Michigan, No. 34.

———. 1952. *Natural Communities.* University of Michigan Press, Ann Arbor, Mich.

DILL, HOMER R., and WILLIAM ALANSON BRYAN. 1912. "Report of an Expedition to Laysan Island in 1911," *United States Department of Agriculture, Bureau of Biological Survey, Bulletin,* 42:1–30.

DOBZHANSKY, T. 1941. *Genetics and the Origin of the Species.* Columbia University Press, New York.

EICHLER, WOLFDIETRICH. 1946. "Problem der Mallophagenforschung," *Die Voegel der Heimat,* 16:205–217.

ELTON, CHARLES. 1936. *Animal Ecology.* The Macmillan Co., New York.

EMLEN, J. T., JR. 1936. "Age Determination in the American Crow," *Condor,* 38:99–102.

———. 1941. "Cliff Swallow Colonies of the Central Sacramento Valley in 1941," *Condor,* 43:248.

———. 1942. "Notes on a Nesting Colony of Western Crows," *Bird-Banding,* 13:143–154.

———. 1950. "Techniques for Observing Bird Behavior Under Natural Conditions," *Annals of the New York Academy of Science,* 51:1103–1112.

———. 1955. "The Study of Behavior in Birds," in *Recent Studies in Avian Biology.* University of Illinois Press, Urbana, Ill.

ERICKSON, JOHN G. 1955. "Flight Behavior of Procellariiformes," *Auk,* 72: 415–420.

ERRINGTON, PAUL L. 1930. "The Pellet Analysis Method of Raptor Food Habits Study," *Condor,* 32:292–296.

———. 1937. "What Is the Meaning of Predation?" *Smithsonian Report for 1936,* pp. 243–252.

———. 1945. "Some Contributions of a Fifteen-Year Local Study of the Northern Bob-white to a Knowledge of Population Phenomena," *Ecological Monographs,* 15:1–34.

———. 1946. "Predation and Vertebrate Populations," *Quarterly Review of Biology,* 21:144–177, 221–245.

EVANS, A. H. 1899. *Birds.* Macmillan & Co., Ltd., London.

FARNER, DONALD S. 1949. "Age Groups and Longevity in the American Robin: Comments, Further Discussion, and Certain Revisions," *Wilson Bulletin,* 61:68–81.

FAUTIN, REED W. 1940. "The Establishment and Maintenance of Territories by the Yellow-headed Blackbird in Utah," *Great Basin Naturalist,* 1:75–91.

———. 1941. "Incubation Studies of the Yellow-headed Blackbird," *Wilson Bulletin,* 53:107–122.

FINGS, HUBERT, and JOSEPH JUMBER. 1954. "Preliminary Studies on the Use of Specific Sound to Repel Starlings (*Sturnus vulgaris*)," *Science,* 119: 318–319.

FISHER, HARVEY I. 1940. "The Occurrence of Vestigial Claws on the Wings of Birds," *American Midland-Naturalist,* 23:234–243.

———. 1944. "The Skulls of Cathartid Vultures," *Condor,* 46:272–296.

———. 1948. "The Question of Avian Introductions in Hawaii," *Pacific Science,* 2:59–64.

FISHER, JAMES. 1939. *Birds as Animals.* William Heinemann, Ltd., London.

———. 1951. *Watching Birds.* Penguin Books, Ltd., Harmondsworth, England.

FISHER, R. A. 1930. *The Genetical Theory of Natural Selection.* Clarendon Press, London.

FITCH, FRANK WILLIAMS, JR. 1950. "Life History of Ecology of the Scissor-tailed Flycatcher, *Muscivora forficata,*" *Auk,* 67:145–168.

FLOWER, STANLEY SMITH. 1938. "Further Notes on the Duration of Life in Animals–IV Birds," *Proceedings of the Zoological Society of London,* Series A, pp. 195–235.

FORBUSH, E. H. 1927. *Useful Birds and Their Protection.* Massachusetts State Board of Agriculture, Boston.

FRENCH, NORMAN R. 1954. "Notes on Breeding Activities and on Gular Sacs in the Pine Grosbeak," *Condor,* 56:83–85.

FRIEDMANN, HERBERT. 1922. "The Weaving of the Red-billed Weaver Bird in Captivity," *Zoologica,* 2:355–372.

———. 1929. *The Cowbirds.* Charles C Thomas, Springfield, Ill.

———. 1930. "Social Parasitism in Birds," *Smithsonian Institution Report for 1929,* pp. 363–382.

FRIEDMANN, HERBERT, and MALCOLM DAVIS. 1938. "Left-handedness in Parrots," *Auk,* 55:478–480.

GABRIELSON, IRA N. 1941. *Wildlife Conservation.* The Macmillan Co., New York.

GARDNER, LEON L. 1925. "The Adaptive Modifications and the Taxonomic Value of the Tongue in Birds," *Proceedings of the United States National Museum*, 67: No. 2591.

GAUSE, G. F. 1934. *The Struggle for Existence.* The Williams & Wilkins Co., Baltimore.

GERSTELL, RICHARD, and WILLIAM H. LONG. 1939. *Physiological Variations in Wild Turkeys and Their Significance in Management.* Pennsylvania Game Commission, Research Bulletin No. 2.

GIBB, JOHN. 1950. "The Breeding Biology of the Great and Blue Titmice," *Ibis*, 92:507–539.

GOWER, CARL. 1936. "The Cause of Blue Color as Found in the Bluebird (*Sialia sialis*) and Blue Jay (*Cyanocitta cristata*)," *Auk*, 53:178–183.

GRANGE, WALLACE B. 1949. *Wisconsin Grouse Problems.* Wisconsin Conservation Department, Madison, Wisconsin.

GRASSE, PIERRE-P. 1950. *Traité de Zoologie: Oiseaux.* Vol. 15. Masson et Cie, Paris.

GREGORY, JOSEPH T. 1952. "The Jaws of the Cretaceous Toothed Birds, *Ichthyornis* and *Hesperornis*," *Condor*, 54:73–88.

GREGORY, WILLIAM K. 1951. *Evolution Emerging.* The Macmillan Co., New York.

GRIFFIN, DONALD R. 1952. "Bird Navigation," *Biological Reviews of the Cambridge Philosophical Society*, 26:359–393.

GRINNELL, JOSEPH. 1904. "The Origin and Distribution of the Chestnut-backed Chickadee," *Auk*, 21:364–382.

———. 1917. "Field Tests of Theories Concerning Distributional Control," *American Naturalist*, 51:115–128.

———. 1936. "Uphill Planters," *Condor*, 38:80–82.

GRISCOM, LUDLOW. 1945. *Modern Bird Study.* Harvard University Press, Cambridge, Mass.

GRISWOLD, JOHN A. 1953. "How Long Do Birds Live?" *Modern Game Breeding and Hunting Club News*, 23: No. 4.

GROSS, A. O. 1947. "Cyclic Invasions of the Snowy Owl and the Migration of 1945–1948," *Auk*, 64:584–601.

HAMERSTROM, FRANCES. 1942. "Dominance in Winter Flocks of Chickadees," *Wilson Bulletin*, 54:32–42.

HANKIN, E. H. 1913. *Animal Flight.* Iliffe & Sons, Ltd., London.

HANN, HARRY W. 1937. "Life History of the Oven-bird in Southern Michigan," *Wilson Bulletin*, 49:145–237.

———. 1941. "The Cowbird at the Nest," *Wilson Bulletin*, 53:211–221.

HARDY, ROSS. 1945. "Breeding Birds of the Pigmy Conifers in the Book Cliff Region of Eastern Utah," *Auk*, 62:523–542.

HARTMAN, FRANK A. 1946. "Adrenal and Thyroid Weights in Birds," *Auk*, 63:42–64.

———. 1955. "Heart Weight in Birds," *Condor*, 57:221–238.

HAYNE, DON. W. 1949. "An Examination of the Strip Census Method for Estimating Animal Populations," *Journal of Wildlife Management*, 13:145–157.

HAZELHOFF, E. H. 1951. "Structure and Function of the Lung of Birds," *Poultry Science*, 30:3–10.

HEADSTROM, RICHARD. 1949. *Birds' Nests: A Field Guide.* Ives Washburn, Inc., New York.

HEALD, F. D., and R. A. STUDHALTER. 1914. "Birds as Carriers of the Chestnut-Blight Fungus," *Journal of Agricultural Research,* 2:405–422.

HEAPE, WALTER. 1932. *Emigration, Migration, and Nomadism.* W. Heffer & Sons, Ltd., Cambridge, England.

HEILMANN, GERHARD. 1927. *The Origin of Birds.* Appleton-Century-Crofts, Inc., New York.

HENDERSON, JUNIUS. 1927. *The Practical Value of Birds.* The Macmillan Co., New York.

HERMAN, C. M. 1938. "The Relative Incidence of Blood Protozoa in Some Birds from Cape Cod," *Transactions of the American Microscopical Society,* 57:132–141.

———. 1944. "The Blood Protozoa of North American Birds," *Bird-Banding,* 15:89–112.

HERMS, W. B. 1950. *Medical Entomology.* The Macmillan Company, New York.

HERRICK, FRANCIS HOBERT. 1911. "Nests and Nest Building in Birds," *Journal of Animal Behavior,* 1:159–192, 244–277, 335–373.

———. 1935. *Wild Birds at Home.* Appleton-Century-Crofts, Inc., New York.

HESS, GERTRUDE. 1951. *The Bird: Its Life and Structure.* Greenberg, Pubisher, New York.

HESSE, RICHARD, W. C. ALLEE, and KARL P. SCHMIDT. 1951. *Ecological Animal Geography.* John Wiley & Sons, Inc., New York.

HICKEY, JOSEPH J. 1943. *A Guide to Bird Watching.* Oxford University Press, New York.

HINGSTON, R. W. G. 1926. "Animal Life at High Altitudes," *Smithsonian Report for 1925,* pp. 337–347.

HOCHBAUM, A. H. 1944. *The Canvas-back on a Prairie Marsh.* American Wildlife Institute, Washington, D. C.

HOPKINS, ANDREW DELMAR. 1938. *Bioclimatics.* United States Department of Agriculture, Miscellaneous Publications No. 280.

HOPKINS, G. H. E. 1942. "The Mallophaga as an Aid to the Classification of Birds," *Ibis,* 6 (Series 14):94–106.

HORNADAY, WILLIAM T. 1913. *Our Vanishing Wildlife.* New York Zoological Society, New York.

HOWARD, H. ELIOT. 1929. *An Introduction to the Study of Bird Behavior.* Cambridge University Press, London.

———. 1948. *Territory in Bird Life.* E. P. Dutton & Co., Inc., New York.

HOWARD, HILDEGARDE. 1930. "A Census of the Pleistocene Birds of Rancho La Brea from Collections in the Los Angeles Museum," *Condor,* 32:81–88.

———. 1947. "A Preliminary Survey of Trends in Avian Evolution from Pleistocene to Recent Times," *Condor,* 49:10–13.

HUDSON, GEORGE ELFORD. 1937. "Studies on the Muscles of the Pelvic Appendage of Birds," *American Midland-Naturalist,* 18:1–108.

HUFF, C. G. 1939. "A Survey of Blood Parasites in Birds Caught for Banding Purposes," *Journal of the American Veterinary Medicine Association,* 94: 615–620.

HUTCHINSON, GEORGE EVELYN. 1950. "The Biogeochemistry of Vertebrate Excretion," *Bulletin American Museum of Natural History, New York,* 96:1–554.

HUXLEY, J. S. 1932. *Problems of Relative Growth.* Methuen & Co., Ltd., London.

HYMAN, LIBBIE HENRIETTA. 1942. *Comparative Vertebrate Anatomy.* University of Chicago Press, Chicago.

———. 1951. *The Invertebrates.* 3 vols. McGraw-Hill Book Co., Inc., New York.

INGRAHAM, SYDNEY E. 1938. "Instinctive Music," *Auk,* 55:614–628.

JACKSON, A. T. 1938. *Picture-Writing of Texas Indians.* University of Texas Publication, Anthropological Papers, No. 3809.

JELLISON, WILLIAM L. 1940. "The Burrowing Owl as a Host to the Argasis Tick, *Ornithodorus parkeri,*" *Public Health Reports,* 55:206–208.

JENKINS, DALE W. 1944. "Territory as a Result of Despotism and Social Organization in Geese," *Auk,* 61:30–47.

JOHNSTON, VERNA R. 1947. "Breeding Birds of the Forest Edge in Illinois," *Condor,* 49:45–53.

JOHNSON, DAVID W. 1956. "The Annual Reproductive Cycle of the California Gull," *Condor,* 58:134–162.

JOHNSTON, RICHARD F. 1954. "Variation in Breeding Season and Clutch Size in Song Sparrows of the Pacific Coast," *Condor,* 56:268–273.

JOLLIE, MALCOLM. 1947. "Plumage Changes in the Golden Eagle," *Auk,* 64: 549–576.

JONES, BRADLEY. 1950. *Elements of Practical Aerodynamics.* John Wiley & Sons, Inc., New York.

KALELA, OLAVI. 1949. "Changes in Geographic Ranges in the Avifauna of Northern and Central Europe in Relation to Recent Changes in Climate," *Bird-Banding,* 20:70–103.

KALMBACH, E. R. 1934a. "Field Observation in Economic Ornithology," *Wilson Bulletin,* 46:73–90.

———. 1934b. *Western Duck Sickness: A Form of Botulism.* United States Department of Agriculture, Technical Bulletin No. 411.

KELSO, LEON. 1940. "Variation of the External Ear-Opening in the Strigidae," *Wilson Bulletin,* 52:24–29.

KENDEIGH, S. CHARLES. 1934. "The Role of Environment in the Life of the Bird," *Ecological Monographs,* 4:299–417.

———. 1939. "The Relation of Metabolism to the Development of Temperature Regulation in Birds," *Journal of Experimental Zoology,* 82:419–438.

———. 1940. "Factors Affecting Length of Incubation," *Auk,* 57:499–513.

———. 1941. "Length of Day and Energy Requirements for Gonad Development and Egg-laying in Birds," *Ecology,* 22:237–248.

———. 1944. "Measurement of Bird Populations," *Ecological Monographs,* 14:67–106.

———. 1945a. "Nesting Behavior of Wood Warblers," *Wilson Bulletin,* 57: 145–164.

———. 1945b. "Community Selection by Birds on the Helderberg Plateau of New York," *Auk,* 62:418–436.

———. 1945c. "Resistance to Hunger in Birds," *Journal of Wildlife Management,* 9:217–226.

——. 1949. "Effect of Temperature and Season on Energy Resources of the English Sparrow," *Auk,* 66:113–127.

———. 1952. "Parental Care and Its Evaluation in Birds," *Illinois Biological Monographs,* 22:1–356.

Koford, Carl B. 1953. *The California Condor.* National Audubon Society, Research Report No. 4.

Kortright, Francis H. 1942. *The Ducks, Geese, and Swans of North America.* American Wildlife Institute, Washington, D. C.

Kramer, Gustav. 1952. "Experiments on Bird Orientation," *Ibis,* 94:265–285.

Küchemann, D., and E. von Host. 1941. "Zur Aerodynamik des Tierfluges," *Luftwissen,* 8:277–282.

Lack, David. 1940. "Courtship Feeding in Birds," *Auk,* 57:169–178.

———. 1944. "Ecological Aspects of Species-Formation in Passerine Birds," *Ibis,* 86:260–286.

———. 1946. *The Life of the Robin.* H. F. & G. Witherby, Ltd., London.

———. 1947, 1948. "The Significance of Clutch Size," *Ibis,* 89:302–352, 90: 25–45.

———. 1950. "Breeding Seasons in the Galapagos," *Ibis,* 92:268–278.

Laskey, Amelia R. 1950. "Cowbird Behavior," *Wilson Bulletin,* 62:157–174.

Lee, Douglas H. K. 1948. "Heat and Cold," *Annual Review of Physiology,* 10:365–386.

Lee, Douglas H. K., and Ralph W. Phillips. 1948. "Assessment of the Adaptability of Livestock to Climatic Stress," *Journal of Animal Science,* 7:391–425.

Lee, Fanny, and Clyde E. Keeler. 1951. "Pigment Variations and Their Correlates in Birds," *Auk,* 68:80–85.

Lehrman, Daniel S. 1953. "A Critique of Konrad Lorenz's Theory of Instinctive Behavior," *Quarterly Review of Biology,* 28:337–363.

Leopold, Aldo. 1933. *Game Management.* Charles Scribner's Sons, New York.

Leopold, A. Starker. 1944. "The Nature of Heritable Wildness in Turkeys," *Condor,* 46:133–197.

———. 1950. "Vegetation Zones of Mexico," *Ecology,* 31:507–518.

Lesher, S. W., and S. Charles Kendeigh. 1941. "Effect of Photoperiod on Molting of Feathers," *Wilson Bulletin,* 53:169–180.

Lincoln, Frederick C. 1939. *The Migration of American Birds.* Doubleday & Co., Inc., New York.

———. 1947. *Manual for Banders.* United States Department of the Interior, Fish and Wildlife Service, Washington, D. C.

———. 1950. *Migration of Birds.* United States Department of the Interior, Fish and Wildlife Service, Circular No. 16.

Linsdale, Jean M. 1928. "A Method of Showing Relative Frequency of Occurrence of Birds," *Condor,* 30:180–184.

———. 1936a. "Coloration of Downy Young and of Nest Linings," *Condor,* 38:111–117.

———. 1936b. "Frequency of Occurrence of Birds in Northern Michigan," *Wilson Bulletin,* 48:158–163.

———. 1938. "Bird Life in Nevada with Reference to Modifications in Structure and Behavior," *Condor,* 40:173–180.

Long, William H. 1939. "The Heat Production and Muscular Activity of Two Strains of Wild Turkeys," *Pennsylvania Game Commission, Research Bulletin,* 2:20–60.

Lorenz, Konrad Z. 1952. *King Solomon's Ring: New Light on Animal Ways.* Crowell Publishing Co., New York.

Lowery, George H., Jr. 1951. "A Quantitative Study of the Nocturnal Migration of Birds," *University of Kansas, Museum of Natural History Publications,* 3:361–472.

MANGELS, FREDERICK P. 1938. "Colored Bands, Methods for Using Bands and Arranging Data," *Bird-Banding*, 9:94–97.

MARSHALL, A. J. 1950. "The Function of the Bower of the Satin Bower-Bird in the Light of Experimental Modification of the Breeding Cycle," *Nature*, 165:388–390.

MARSHALL, JOE T. 1948. "Ecologic Races of Song Sparrows in the San Francisco Bay Region," *Condor*, 50:193–215.

MARSHALL, WILLIAM H. 1946. "Cover Preferences, Seasonal Movements, and Food Habits of Richardson's and Ruffed Grouse in Southern Idaho," *Wilson Bulletin*, 58:42–52.

MASON, EDWIN A. 1944. "Parasitism by *Protocalliphora* and Management of Cavity-Nesting Birds," *Journal of Wildlife Management*, 8:232–247.

MATHEW, WILLIAM DILLER. 1939. *Climate and Evolution*. New York Academy of Sciences, Special Publications.

MATHEWS, F. SCHUYLER. 1921. Field Book of Wild Birds and Their Music. G. P. Putnam's Sons, New York.

MATHEWS, G. V. T. 1955. *Bird Navigation*. Cambridge University Press, London.

MAYFIELD, HAROLD. 1953. A Census of the Kirtland's Warbler, *Auk*, 70:17–20.

MAYR, ERNST. 1935. "Bernard Altum and the Territory Theory," *Proceedings of the Linnean Society of New York*, pp. 45–46.

———. 1939. "The Sex Ratio in Wild Birds," *American Naturalist*, 73:156–179.

———. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York.

———. 1946. "History of the North American Bird Fauna," *Wilson Bulletin*, 58:3–41.

MAYR, ERNST, and CHARLES VAURIE. 1948. "Evolution in the Family *Dicruridae* (Birds)," *Evolution*, 2:238–265.

MAYR, ERNST, and DEAN AMADON. 1951. *A Classification of Recent Birds*. American Museum Novitiates, No. 1496.

MAYR, ERNST, E. G. LINDSEY, and R. L. USINGER. 1953. *Methods and Principles of Systematic Zoology*. McGraw-Hill Book Co., Inc., New York.

MEINERTZHAGEN, R. 1955. "The Speed and Altitude of Bird Flight," *Ibis*, 97:81–117.

MICHENER, HAROLD, and JOSEPHINE R. MICHENER. 1940. "The Molt of House Finches of the Pasadena Region, California," *Condor*, 42:140–153.

MICHENER, JOSEPHINE R. 1951. "Territorial Behavior and Age Composition in a Population of Mockingbirds at a Feeding Station," *Condor*, 53:276–283.

MILLER, ALDEN H. 1934. "The Vocal Apparatus of Some North American Owls," *Condor*, 36:204–213.

———. 1939. "Analysis of Some Hybrid Populations of Juncos," *Condor*, 41:211–214.

———. 1940. "An Early Record of the Dickcissel in Arizona," *Condor*, 42:125.

———. 1941a. "The Significance of Molt Centers Among the Secondary Remiges in the Falconiformes," *Condor*, 43:113–115.

———. 1941b. "The Buccal Food-Carrying Pouches of the Rosy Finch," *Condor*, 43:72–73.

———. 1942. "Habitat Selection Among Higher Vertebrates and Its Relation to Intraspecies Variation," *American Naturalist*, 76:25–35.

MILLER, ALDEN H. 1943. "Census of a Colony of Caspian Terns," *Condor*, 45:220–225.

MILLER, ALDEN H., and LAWRENCE V. COMPTON. 1939. "Two Fossil Birds from the Lower Miocene of South Dakota," *Condor*, 41:153–156.

MILLER, LOYE. 1942. "Succession in the Cathartine Dynasty," *Condor*, 44: 212–213.

MILLER, ROBERT C. 1922. "The Significance of the Gregarious Habit," *Zoology*, 3:122–126.

MILLS, HERBERT R. 1944. "The Log of Whiskey Stump, Water-Fowl Ecology," *The Florida Naturalist*, 18:2–8.

MISKIMEN, MILDRED. 1951. "Sound Production in Passerine Birds," *Auk*, 68: 493–504.

MITCHELL, P. CHALMERS. 1911. "On the Longevity and Relative Viability in Mammals and Birds, with a Note on the Theory of Longevity," *Proceedings of the Zoological Society of London*, pp. 425–458.

MITCHELL, R. T., H. P. BLAGBROUGH, and R. C. VAN ETTEN. 1953. "The Effects of DDT Upon the Survival and Growth of Nestling Songbirds," *Journal of Wildlife Management*, 17:45–54.

MOORE, A. D. 1945. "Winter Night Habits of Birds," *Wilson Bulletin*, 57: 253–260.

———. 1951. "Adaptation of Animals to Climatic Extremes: A Review," *Wilson Bulletin*, 63:358–362.

MOREAU, R. E. 1935. "A Synecological Study of Usambara, Tanganyika Territory, with Particular Reference to Birds," *Journal of Ecology*, 23:1–43.

———. 1950. "The Breeding Seasons of African Birds: 2, Sea Birds," *Ibis*, 92:419–433.

———. 1954. "The Main Vicissitudes of the European Avifauna Since the Pliocene," *Ibis*, 96:411–413.

MOREAU, R. E., and W. M. MOREAU. 1940. "Incubation and Fledgling Periods of African Birds," *Auk*, 57:313–325.

MORRIS, PERRY A. 1938. *Nature Photography Around the Year.* Appleton-Century-Crofts, Inc., New York.

MOSELEY, EDWIN L. 1946. "Variations in Bird Populations of Ohio and Nearby States," *Ohio Journal of Science*, 46:308–322.

MURPHY, ROBERT CUSHMAN. 1925. *Bird Islands of Peru.* G. P. Putnam's Sons, New York.

———. 1936. *Oceanic Birds of South America.* 2 vols. American Museum of Natural History, New York.

———. 1951. *The Population of the Wedge-tailed Shearwater.* American Museum of Novitiates, No. 1512.

NEFF, JOHNSON A. 1947. "Habits, Food, and Economic Status of the Band-tailed Pigeon," *North American Fauna*, 58.

NERO, ROBERT W. 1954. "Plumage Aberrations of the Redwing (*Agelaius phoeniceus*)," *Auk*, 71:137–155.

NEWMAN, H. H. 1939. *The Phylum Chordata.* The Macmillan Co., New York.

NEWTON, ALFRED. 1893–1896. *A Dictionary of Birds.* Adam & Charles Black, London.

NICE, MARGARET MORSE. 1937, 1943. "Studies in the Life Histories of the Song Sparrow, I and II." *Transactions of the Linnean Society of New York*, 4:1–247, 6:1–328.

———. 1938. "The Biological Significance of Body Weight," *Bird-Banding*, 9:1–11.

———. 1941a. "The Role of Territory in Bird Life," *American Midland-Naturalist*, 26:441–487.

———. 1941b. *The Watcher at the Nest*. The Macmillan Co., New York.

———. 1954. "Problems of Incubation Periods in North American Birds," *Condor*, 56:173–197.

NICE, MARGARET MORSE, and JOOST TER PELKWYK. 1940. "'Anting' by the Song Sparrow," *Auk*, 57:520–522.

———. 1941. "Enemy Recognition by the Song Sparrow," *Auk*, 58:195–214.

NICHOLSON, E. M. 1932. *The Art of Bird Watching*. Charles Scribner's Sons, New York.

NICHOLSON, E. M., and LUDWIG KOCH. 1936. *Songs of Wild Birds*. H. F. & G. Witherby, Ltd., London.

NOBLE, G. K. 1936. "Courtship and Sexual Selection of the Flicker (*Colaptes auratus luteus*)," *Auk*, 53:269–282.

NOPSCA, F. 1907. "Ideas on the Origin of Flight," *Proceedings of the Zoological Society of London*, pp. 223–236.

———. 1923. "On the Origin of Flight in Birds," *Proceedings of the Zoological Society of London*, pp. 463–477.

ODUM, EUGENE P. 1942–1943. "Annual Cycle of the Black-capped Chickadee," *Auk*, 58:314–333, 518–535, 59:499–531.

———. 1943. "Some Physiological Variations in the Black-capped Chickadee," *Wilson Bulletin*, 55:178–191.

———. 1949. "Weight Variation in Wintering White-throated Sparrows in Relation to Temperature and Migration," *Wilson Bulletin*, 61:3–14.

———. 1953. *Fundamentals of Ecology*. W. B. Saunders Co., Philadelphia.

OLDYS, H. W. 1902. "Parallel Growth of Bird and Human Music," *Harper's Magazine*, 105:474–478.

OOSTING, HENRY J. 1948. *The Study of Plant Communities: An Introduction to Plant Ecology*. W. H. Freeman Co., San Francisco.

PALMER, R. S. 1941. "A Behavior Study of the Common Tern," *Proceedings of the Boston Society of Natural History*, 42:1–119.

PALMGREN, P. 1944. "Studien über die Tagesrhythmik gekäfigter Zugvogel," *Zeitschrift für Tierpsychologie*, 6:44–86.

PARKER, JESSE E., FRED F. MCKENZIE, and H. L. KEMPSTER. 1942. *Fertility in the Male Domestic Fowl*. Missouri Agricultural Experiment Station, Research Bulletin No. 347.

PARKES, KENNETH C. 1951. "The Genetics of the Golden-winged Warbler X Blue-winged Warbler Complex," *Wilson Bulletin*, 63:5–15.

PATTON, BRADLEY M. 1952. *Early Embryology of the Chick*. The Blakiston Co., Philadelphia.

PEARSON, OLIVER T. 1950. "The Metabolism of Hummingbirds," *Condor*, 52:145–152.

———. 1953. "Metabolism of Hummingbirds," *Scientific American*, 188: 69–72.

PEARSON, T. GILBERT. 1933. "Fifty Years of Bird Protection in the United States," in *Fifty Years' Progress of American Ornithology, 1883–1933*. Lancaster, Pa.

———. 1937. *Adventures in Bird Protection*. Appleton-Century-Crofts, Inc., New York.

PERCY, LORD WILLIAM. 1951. *Three Studies in Bird Character.* Country Life, Ltd., London.

PETERS, HAROLD S. 1936. "A List of External Parasites from Birds of the Eastern Part of the United States," *Bird-Banding,* 7:9–27.

PETERS, JAMES L. 1931. *Check-List of Birds of the World.* Harvard University Press, Cambridge, Mass.

PETERSON, ROGER TORY. 1947. *A Field Guide to Birds.* Houghton Mifflin Co., Boston.

PETERSON, ROGER TORY, GUY MONTFORT, and P. A. D. HOLLOM. 1954. *A Field Guide to Birds of Britain and Europe.* Houghton-Mifflin Co., Boston.

PETTINGILL, OLIN SEWALL, JR. 1939. "History of One Hundred Nests of Arctic Tern," *Auk,* 56:420–428.

———. 1951. *A Guide to Bird Finding East of the Mississippi.* Oxford University Press, New York.

———. 1953. *A Guide to Bird Finding West of the Mississippi.* Oxford University Press, New York.

———. 1956. *A Laboratory and Field Manual of Ornithology.* Burgess Publishing Co., Minneapolis, Minn.

PICKENS, A. L. 1929. "Bird Pollination Problems in California," *Condor,* 31: 229–232.

PITELKA, FRANK A. 1941. "Distribution of Birds in Relation to Major Biotic Communities," *American Midland-Naturalist,* 25:113–137.

———. 1945. "Pterylography, Molt, and Age Determination of American Jays of the Genus *Aphelocoma,*" *Condor,* 47:229–260.

POOLE, EARL L. 1936. "Relative Wing Weights of Bats and Birds," *Journal of Mammalogy,* 17:412-443.

———. 1938. "Weights and Wing Areas in North American Birds," *Auk,* 55:511–517.

POUGH, RICHARD H. 1940. "Massacred for Millinery," *Bird-Lore,* 42:395–404.

———. 1946. *Audubon Bird Guide (Land Birds).* Doubleday & Co., Inc., New York.

———. 1951. *Audubon Bird Guide (Water Birds).* Doubleday & Co., Inc., New York.

PRESTON, T. W. 1953. "The Shapes of Birds' Eggs," *Auk,* 70:160–182.

PROSSER, C. LADD. 1950. *Comparative Animal Physiology.* W. B. Saunders Co., Philadelphia.

PYCRAFT, W. P. 1910. *A History of Birds.* Methuen & Co., Ltd., London.

QUAY, THOMAS L. 1947. "Winter Birds of Upland Plant Communities," *Auk,* 64:382–388.

———. 1951. *Mourning Dove Studies in North Carolina.* North Carolina Wildlife Resources Commission.

QUIRING, DANIEL P. 1950. *Functional Anatomy of the Vertebrates.* McGraw-Hill Book Co., Inc., New York.

RAISZ, ERVIN. 1948. *General Cartography.* McGraw-Hill Book Co., Inc., New York.

RASPET, AUGUST. 1950. "Performance Measurements of a Soaring Bird," *Aeronautical Engineering Review,* 9:1–4.

RAVENHILL, ALICE. 1944. *An Outline of Arts and Crafts of the Indian Tribes of British Columbia.* Occasional Papers of the British Columbia Provincial Museum, No. 5.

REICHERT, ROBERT J., and ELSA REICHERT. 1951. "Know Your Binoculars," *Audubon Magazine*, 53:45–50, 104–109.

RICHARDSON, FRANK. 1939. Functional Aspects of the Pneumatic System of the California Brown Pelican," *Condor*, 41:13–17.

———. 1942. "Adaptive Modifications for Tree Trunk Foraging in Birds," *University of California Publications in Zoology*, 46:317–368.

RICHARDSON, FRANK, and HARVEY I. FISHER. 1950. "Birds of Moku Manu and Manana Islands off Oahu, Hawaii," *Auk*, 67:285–306.

RICHDALE, L. E. 1939. *Study of a Group of Penguins of Known Age*. Privately Published, Dunedin, New Zealand.

———. 1951. *Sexual Behavior in Penguins*. University of Kansas Press, Lawrence, Kan.

ROBBINS, CHANDLER S., and ROBERT E. STEWART. 1949. "Effects of DDT on Bird Populations of Scrub Forest," *Journal of Wildlife Management*, 13: 11–16.

ROMANOFF, ALEXIS L. 1949. "Critical Periods and Causes of Death in Avian Embryonic Development," *Auk*, 66:264–270.

ROMANOFF, ALEXIS L., and ANASTASIA J. ROMANOFF. 1949. *The Avian Egg*. John Wiley & Sons, Inc., New York.

ROMER, A. S. 1950. *The Vertebrate Body*. W. B. Saunders Co., Philadelphia.

ROTHSCHILD, MERIAM, and THERESA CLAY. 1950. *Fleas, Flukes, and Cuckoos*, William Collins Sons & Co., Ltd., London.

ROTHSCHILD, WALTER. 1897. *Extinct Birds*. Hutchinson & Co., Ltd., London.

ROWAN, WILLIAM. 1931. *The Riddle of Migration*. The Williams & Wilkins Co., Baltimore.

RÜPPEL, W. 1933. "Physiologie und Akustik der Vogelstimme," *Journal für Ornithologie*, 81:433–542.

SAUNDERS, ARETAS A. 1929. *Bird Sing*. New York State Museum Handbook, No. 7.

———. 1948. "The Seasons of Bird Song: The Cessation of Song After the Nesting Season," *Auk*, 65:19–30.

———. 1951. *A Guide to Bird Songs*. Doubleday & Co., Inc., New York.

SAUNDERS, WILLIAM E. 1934. "Losing the Bird Songs," *Auk*, 51:503–506.

SAVILE, D. B. O. 1950. "The Flight Mechanism of Swifts and Hummingbirds," *Auk*, 67:499–504.

SCHELDERUP-EBBE, T. 1935. "Social Behavior of Birds," chap. xx in MURCHISON, *Handbook of Social Psychology*. Clark University Press, Worcester, Mass.

SCHORGER, A. W. 1937. "The Great Wisconsin Passenger Pigeon Nesting of 1871," *Proceedings of the Linnean Society of New York, 1936*, 48:1–26.

———. 1941. "The Bronzed Grackle's Method of Opening Acorns," *Wilson Bulletin*, 53:238–240.

———. 1944. "The Quail in Early Wisconsin," *Transactions of the Wisconsin Academy of Sciences, Arts and Letters*, 36:77–103.

———. 1947. "The Deep Diving of the Loon and Old-Squaw and Its Mechanism," *Wilson Bulletin*, 59:151–159.

———. 1955. *The Passenger Pigeon: Its Natural History and Extinction*. University of Wisconsin Press, Madison, Wis.

SCHWARTZKOPFF, JOHANN. 1955. "On the Hearing of Birds," *Auk*, 72:340–347.

SCOTT, JOHN W. 1942. "Mating Behavior of the Sage Grouse," *Auk*, 59:477–498.

SEIBERT, HENRI C. 1949. "Difference Between Migrant and Non-migrant Birds in Food and Water Intake at Various Temperatures and Photoperiods," *Auk*, 66:128–153.

———. 1951. "Light Intensity and the Roosting Flight of Herons in New Jersey," *Auk*, 88:63–74.

SHARPE, R. BOWDLER. 1874–1898. *Catalogue of Birds in the British Museum.* British Museum, London.

———. 1899–1909. *A Hand-List of the Genera and Species of Birds.* British Museum, London.

SHAW, WILLIAM T. 1936. "Winter Life and Nesting Studies of Hepburn's Rosy Finch in Washington State," *Auk*, 53:9–16.

SHERWOOD, A. WILEY. 1946. *Aerodynamics.* McGraw-Hill Book Co., Inc., New York.

SHUFELDT, R. W. 1890. *The Myology of the Raven (Corvus corax sinuatus).* The Macmillan Co., New York.

———. 1909. *Osteology of Birds.* New York State Museum, Bulletin No. 130.

SHULTZ, LEONARD P., and EDITH M. STERN. 1948. *The Ways of Fishes.* D. Van Nostrand Co., Inc., New York.

SHUMWAY, WALDO. 1948. *Introduction to Vertebrate Embryology.* John Wiley & Sons, Inc., New York.

SIMMS, ERIC. 1952. *Bird Migrants.* Cleaver-Hume Press, Ltd., London.

SIMPSON, GEORGE GAYLORD. 1953. *The Major Features of Evolution.* Columbia University Press, New York.

SIMPSON, GEORGE GAYLORD, and ANNE ROE. 1939. *Quantitative Zoology.* McGraw-Hill Book Co., Inc., New York.

SINNOTT, E. W., L. C. DUNN, and T. DOBZHANSKY. 1950. *Principles of Genetics.* McGraw-Hill Book Co., Inc., New York.

SKUTCH, ALEXANDER F. 1935. "Helpers at the Nest," *Auk*, 52:257–273.

———. 1945. "Incubation and Nestling Periods of Central American Birds," *Auk*, 62:8–37.

———. 1951. "Congeneric Species of Birds Nesting Together in Central America," *Condor*, 53:3–15.

———. 1952. "On the Hours of Laying and Hatching of Birds' Eggs," *Ibis*, 94:49–61.

———. 1953. "How the Male Bird Discovers the Nestlings," *Ibis*, 95:1–37, 505–541.

———. 1954, 1955. "The Parental Stratagems of Birds, *Ibis*, 96:544–564, 97: 118–142.

SLIJPER, E. J. 1950. *De Fliegkunst in het Dierenrijk.* E. J. Brill, Ltd., Leiden, Netherlands.

SMITH, STUART, and ERIC HOSKING. 1955. *Birds Fighting.* Faber & Faber, Ltd., London.

SNYDER, LAURENCE H. 1951. *Principles of Heredity.* D. C. Heath & Co., Boston.

STANLEY, ALLEN J. 1941. "Sexual Dimorphism in the Cowbird, *Molothrus ater*," *Wilson Bulletin*, 53:33–36.

STEWART, ROBERT E., and JOHN W. ALDRICH. 1951. "Removal and Repopulation of Breeding Birds in a Spruce-Fir Forest Community," *Auk*, 68:471–482.

STODDARD, HERBERT L. 1931. *The Bob-White Quail.* Charles Scribner's Sons, New York.

STORER, JOHN H. 1948. *The Flight of Birds.* Cranbrook Institute of Science, Bloomfield Hills, Mich.

STORER, TRACY I. 1951. *General Zoology.* McGraw-Hill Book Co., Inc., New York.

STRESEMANN, ERWIN. 1951. *Die Entwichlung der Ornithologie von Aristotle bis zur Gegenwort.* F. W. Peters, Berlin.

STRONG, REUBEN M. 1939–1946. *A Bibliography of Birds.* Field Museum of Natural History, Zoological Series No. 25.

STURKIE, PAUL D. 1954. *Avian Physiology.* Comstock Publishing Associates, Inc., Ithaca, N. Y.

SUMNER, E. LOWELL, JR. 1935. "A Life History Study of the California Quail, with Recommendations for Conservation and Management," *California Fish and Game,* 21:167–256, 277–342.

SUTTON, GEORGE MIKSCH. 1935. *The Juvenal Plumage and Post-Juvenal Molt in Several Species of Michigan Sparrows.* Cranbrook Institute of Science, Bulletin No. 3.

———. 1946. "Wing-Flashing in the Mockingbird," *Wilson Bulletin,* 58:206–209.

———. 1949. *Studies of the Nesting Birds of the Edwin S. George Reserve, Part I, the Vireos.* University of Michigan, Museum of Zoology, Miscellaneous Publications, No. 74.

———. 1951. "Dispersal of Mistletoe by Birds," *Wilson Bulletin,* 63:235–237.

SYMPOSIUM. 1945. "Bird Distribution and Ecological Concepts," *Wilson Bulletin,* 57:191–201.

TABER, RICHARD D. 1949. "Observations on the Breeding Behavior of the Ring-necked Pheasant," *Condor,* 51:153–175.

TANNER, JAMES T. 1942. The Ivory-billed Woodpecker. National Audubon Society, Research Report No. 1.

TEST, FREDERICK H. 1945. "Molt in Flight Feathers," *Condor,* 47:63–72.

THAYER, GERALD H. 1909. *Concealing Coloration in the Animal Kingdom.* The Macmillan Co., New York.

THOMSON, A. LANDSBOROUGH. 1936. *Bird Migration.* H. F. & G. Witherby, Ltd., London.

———. 1953. "The Study of Visible Migration in Birds," *Ibis,* 95:165–180. (A summary of other papers.)

THOMSON, J. ARTHUR. 1923. *The Biology of Birds.* The Macmillan Co., New York.

THORPE, W. H. 1951. "The Learning Ability of Birds," *Ibis,* 93:1–52, 252–296.

TINBERGEN, N. 1936. "The Function of Sexual Fighting in Birds and the Problem of the Origin of 'Territory,'" *Bird-Banding,* 7:1–8.

———. 1948. "Social Releasers and the Experimental Method Required for Their Study," *Wilson Bulletin,* 60:6–51.

———. 1951. *The Study of Instinct.* Clarendon Press, London.

———. 1953. *Social Behavior in Animals.* Methuen & Co., Ltd., London.

TRAUTMAN, MILTON B., WILLIAM E. BILLS, and EDWARD L. WICKLIFF. 1939. "Winter Losses from Starvation and Exposure of Waterfowl and Upland Game Birds in Ohio and Other Northern States," *Wilson Bulletin,* 51: 86–104.

TWOMEY, ARTHUR C. 1936. "Climographic Study of Certain Introduced and Migratory Birds," *Ecology,* 17:122–132.

VAN DERSAL, WILLIAM R. 1938. Native Woody Plants of the United States, Their Erosion-Control and Wildlife Value. United States Department of Agriculture, Miscellaneous Publication No. 303.

VAN ROSSEM, A. J. 1926. "The California Forms of *Agelaius phoeniceous* (Linnaeus)," *Condor*, 28:215–230.

———. 1927. "Eye Shine in Birds, with Notes on the Feeding Habits of Some Goatsuckers," *Condor*, 29:25–28.

VORHIES, CHARLES T. 1945. *Water Requirements of Desert Animals in the Southwest.* University of Arizona, Technical Bulletin No. 107.

WADKINS, L. A. 1948. "Dyeing Birds for Identification," *Journal of Wildlife Management*, 12:388–391.

WAGNER, HELMUTH O. 1944. "Notes on the Life History of the Emerald Toucanet," *Wilson Bulletin*, 56:65–76.

———. 1945. "Notes on the Life History of the Mexican Violet-Ear," *Wilson Bulletin*, 57:165–187.

———. 1946. "Food and Feeding Habits of Mexican Hummingbirds," *Wilson Bulletin*, 58:69–93.

WALKINSHAW, LAWRENCE H. 1938. "Nesting Studies of the Prothonotary Warbler," *Bird-Banding*, 9:32–46.

———. 1939. "Nesting of the Field Sparrow and Survival of the Young," *Bird-Banding*, 10:107–114, 149–157.

———. 1941. "The Prothonotary Warbler, a Comparison of Nesting Conditions in Tennessee and Michigan," *Wilson Bulletin*, 53:3–21.

WALLS, G. L. 1942. *The Vertebrate Eye.* Cranbrook Institute of Science, Bloomfield Hills, Mich.

WEAVER, J. E., and F. E. CLEMENTS. 1938. *Plant Ecology.* McGraw-Hill Book Co., Inc., New York.

WEBSTER, R. L. 1951. *New Insecticides: Their Use, Limitations, and Hazards to Human Health.* Washington Agricultural Experiment Stations, Circular No. 64.

WEIMAN, H. L. 1949. *An Introduction to Vertebrate Embryology.* McGraw-Hill Book Co., Inc., New York.

WELTER, WILFRED A. 1936. "Feather Arrangement, Development, and Molt of the Long-billed Marsh Wren," *Wilson Bulletin*, 48:256–269.

WESTON, HENRY G., JR. 1947. "Breeding Behavior of the Blackheaded Grosbeak," *Condor*, 49:54–73.

———. 1948. "Spring Arrival of Summer Residents in the Berkeley Area, California," *Condor*, 50:81–82.

WETMORE, ALEXANDER. 1921. *A Study of Body Temperature of Birds.* Smithsonian Miscellaneous Collections, 72: No. 12.

———. 1927a. "A Method for Keeping Notes and Files Dealing with Ornithology," *Condor*, 29:109–111.

———. 1927b. *The Migration of Birds.* Harvard University Press, Cambridge, Mass.

———. 1933. *Pliocene Bird Remains from Idaho.* Smithsonian Miscellaneous Collections, 87: No. 3228.

———. 1936. "The Number of Contour Feathers in Passeriform and Related Birds," *Auk*, 53:159–169.

———. 1951. *A Revised Classification for the Birds of the World.* Smithsonian Miscellaneous Collections, 117: No. 4.

WILLIAMS, G. R. 1953. "The Dispersal from New Zealand and Australia of Introduced European Passerines," *Ibis*, 95:676–692.

WING, ANNE HINSHAW. 1951. "Notes on the Song Series of a Hermit Thrush in the Yukon," *Auk*, 68:189–193.

WING, LEONARD W. 1940. "A Game Survey of Northwestern Tennessee," *Journal of the Tennessee Academy of Science*, 15:309–320.

———. 1941. "Size of Bird Flocks in Winter," *Auk*, 58:188–194.

———. 1943a. "The Spread of the Starling and English Sparrow," *Auk*, 60: 74–87.

———. 1943b. "Relative Distribution of Mallard and Black Duck in Winter," *Auk*, 60:438–439.

———. 1943c. "Freezing and Thawing Dates of Lakes and Rivers as Phenological Indicators," *Monthly Weather Review*, 71:149–158.

———. 1946a. "Drumming Flight in the Blue Grouse and Courtship Characters of the Tetraonidae," *Condor*, 48:154–157.

———. 1946b. "Species Association in Winter Groups," *Auk*, 63:508–511.

———. 1947. "Seasonal Movements of Blue Grouse," *Transactions of the Twelfth North American Wildlife Conference*, pp. 504–510.

———. 1949. "Breeding Birds of Virgin Palouse Prairie," *Auk*, 66:38–41.

———. 1951. *Practice of Wildlife Conservation.* John Wiley & Sons, Inc., New York.

———. 1953a. "Cycles in Flight Years of Snowy Owl, Evening Grosbeak, and Pine Grosbeak," *Journal of Cycle Research*, 2.52.

———. 1953b. "Cycles of European Partridge Abundance," *Journal of Cycle Research*, 2:56–76.

———. 1954. "Global Pattern of 4.222-Year Cycles in Temperature," *Journal of Cycle Research*, 3:55–83.

WING, LEONARD W., JAMES BEER, and WAYNE TIDYMAN. 1944. "Brood Habits and Growth of Blue Grouse," *Auk*, 61:426–440.

WITCHELL, CHARLES A. 1896. *The Evolution of Bird-Song.* Adam & Charles Black, Ltd., London.

WOLFSON, ALBERT. 1945. "The Role of the Pituitary, Fat Deposition, and Body Weight in Bird Migration," *Condor*, 47:95–127.

———. 1952. "Day Length, Migration and Breeding Cycles in Birds," *Scientific Monthly*, 74:191–200.

WOOD, HAROLD B. 1937. "How Far Can a Bird Be Seen?" *Auk*, 54:96–97.

———. 1941. "Fractures Among Birds," *Bird-Banding*, 12:68–72.

———. 1946. "Names of Age Groups of Young Birds," *Bird-Banding*, 17: 27–33.

WOOD, NORMAN A., and A. D. TINKER. 1914. *Fifty Years of Bird Migration in the Ann Arbor Region of Michigan, 1880–1930.* Occasional Papers of the Museum of Zoology, University of Michigan, No. 280.

WOODCOCK, ALFRED H. 1942. "Soaring Over the Open Sea," *Scientific Monthly*, 55:226–232.

WORTH, C. BROOKE. 1940a. "Egg Volumes and Incubation Periods," *Auk*, 57: 44–60.

———. 1940b. "Birds and Human Disease," *Wilson Bulletin*, 61:183–186.

YOCOM, CHARLES F. 1951. *Waterfowl and Their Food Plants in Washington.* University of Washington Press, Seattle.

YOUNG, J. Z. 1950. *The Life of Vertebrates.* Clarendon Press, London.

SUGGESTED PERIODICAL REFERENCES[1]

Alauda, 1929—France
Archives Suisses D'Ornithologie, 1932—Switzerland
Audubon Magazine, 1899—United States
Auk, 1883 (1876)—United States and Canada
Beitrage zur Fortplanzungsbiologie der Vogel, 1924—Germany
Biological Abstracts, 1926—United States
Bird-Banding, 1929 (1924)—United States
British Birds, 1907—Great Britain
Bulletin of the British Ornithologists' Club, 1892—Great Britain
Canadian Field-Naturalist, 1887—Canada
Condor, 1899—California
El Hornero, 1917—Argentina
Emu, 1901—Australia
Ibis, 1859—Great Britain
Journal für Ornithologie, 1854—Germany
Le Gerfaut, 1911—Belgium
L'Oiseau, 1931—France
Murrelet, 1920—United States and Canada
Ornis Fennica, 1924—Finland
Ornithologische Monatsberichte, 1894—Germany
Vogelzug, 1930—Germany
Wilson Bulletin, 1888—United States and Canada
Zoological Record (*Aves* Section), 1864—Great Britain

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[1] With beginning date and country of publication. *The Zoological Record* is a bibliography.

Appendix II

Bird Orders and Families of the World

This Appendix supplies in brief form the names of bird orders and families of the world, their general range, and the number of species reported. The orders and families follow the classification of Wetmore (1951); the number of species is largely that of Mayr (1946).[*]

- Class AVES, Birds
  - Subclass ARCHAEORNITHES, Ancestral Birds
    - Order ARCHAEOPTERYGIFORMES, *Archaeopteryx*
      - Family ARCHAEOPTERYGIDAE (fossil)
  - Subclass NEORNITHES, True Birds
    - HESPERORNITHIFORMES, HESPERORNITHES
      - HESPERORNITHIDAE, *Hesperornis, Hargeria* (fossil)
      - ENALIORNITHIDAE (fossil)
      - BAPTORNITHIDAE (fossil)
    - ICHTHYORNITHIFORMES, ICHTHYORNITHES
      - ICHTHYORNITHIDAE, *Ichthyornis* [†] (fossil)
      - APATORNITHIDAE (fossil)
    - SPHENISCIFORMES, Penguins
      - SPHENISCIDAE, Penguins (Antarctic, 17)
    - CAENAGNATHIFORMES [‡] (fossil)
    - STRUTHIONIFORMES, Ostriches
      - ELEUTHERORNITHIDAE (fossil)
      - STRUTHIONIDAE, Ostriches (Africa, Asia, 1)

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[*] Cf., Mayr and Amadon (1951).

[†] The lower jaw of the fossil upon which Ichthyornis is based is reported to be reptilian rather than of a bird (Gregory, 1952).

[‡] Possibly not a bird.

- RHEIFORMES, Rheas
  - RHEIDAE, Rheas (South America, 2)
- CASUARIIFORMES, Cassowaries, Emus
  - CASUARIIDAE, Cassowaries (Australia, 3)
  - DROMICEIDAE, Emus (Australia, 2)
  - DROMORNITHIDAE (fossil)
- AEPYORNITHIFORMES, Elephant-birds
  - AEPYORNITHIDAE, *Aepyornis* (fossil and extinct)
- DINORNITHIFORMES, Moas
  - DINORNITHIDAE, Moas (fossil and extinct)
  - ANOMALOPTERYGIDAE, (fossil and extinct)
- APTERYGIFORMES, Kiwis
  - APTERYGIDAE, Kiwis (New Zealand, 3)
- TINAMIFORMES, Tinamous
  - TINAMIDAE, Tinamous (South and Central America, 32)
- GAVIIFORMES, Loons
  - GAVIIDAE, Loons (Northern Hemisphere, 3)
- COLYMBIFORMES, Grebes
  - COLYMBIDAE, Grebes (World-wide, 20)
- PROCELLARIIFORMES, Albatrosses and allies
  - DIOMEDEIDAE, Albatrosses (Oceanic, 14)
  - PROCELLARIIDAE, Shearwaters, Fulmars (World-wide, 56)
  - HYDROBATIDAE, Storm Petrels (Oceanic, 18)
  - PELECANOIDIDAE, Diving Petrels (Southern Hemisphere, 5)
- PELECANIFORMES, Pelicans, Frigates, and allies
  - PHAETHONTIDAE, Tropic-birds (Tropical oceans, 3)
  - PELECANIDAE, Pelicans (World-wide, 6)
  - CYPHORNITHIDAE (fossil)
  - PELAGORNITHIDAE (fossil)
  - SULIDAE, Gannets, Boobies (World-wide, 9)
  - ELOPTERYGIDAE (fossil)
  - PHALACROCORACIDAE, Cormorants (World-wide, 30)
  - ANHINGIDAE, Anhingas (Snake-birds) (Tropics and Subtropics, 1)
  - FREGATIDAE, Frigate-birds (Tropical oceans, 5)
  - ODONTOPTERYGIDAE (fossil)
  - PSEUDODONTORNITHIDAE (fossil)
  - CLADORNITHIDAE (fossil)
- CICONIIFORMES, Herons, Storks, and allies
  - ARDEIDAE, Herons, Bitterns (World-wide, 59)
  - COCHLEARIIDAE, Boat-billed Herons (South and Central America, 1)
  - BALAENICIPITIDAE, Whale-headed Storks (Africa, 1)
  - SCOPIDAE, Hammerheads (Africa, 1)
  - CICONIIDAE, Storks, Jabirus (World-wide, 16)
  - THRESKIORNITHIDAE, Ibises, Spoonbills (World-wide, 28)
  - AGNOPTERIDAE (fossil)
  - SCANIORNITHIDAE (fossil)
  - PHOENICOPTERIDAE, Flamingos (Tropics, 6)

ANSERIFORMES, Waterfowl
- ANHIMIDAE, Screamers (South America, 3)
- PARANYROCIDAE (fossil)
- ANATIDAE, Ducks, Geese, Swans (World-wide, 145)

FALCONIFORMES, Vultures, Hawks, Falcons
- NEOCATHARTIDAE (fossil)
- CATHARTIDAE, New World Vultures (North and South America, 6)
- TERATORNITHIDAE (fossil)
- SAGITTARIIDAE, Secretary-birds (Africa, 1)
- ACCIPITRIDAE, Hawks, Old World Vultures, Harriers (World-wide, 205)
- PANDIONIDAE, Ospreys (World-wide, 1)
- FALCONIDAE, Falcons, Caracaras (World-wide, 58)

GALLIFORMES, Gallinaceous Birds
- MEGAPODIIDAE, Megapodes (Brush-turkeys) (Australia, 10)
- GALLINULOIDIDAE (fossil)
- CRACIDAE, Curassows, Guans, Chachalacas (Texas to South America, 38)
- TETRAONIDAE, Grouse (North America, Eurasia, 18)
- PHASIANIDAE, Pheasants, Quails, Peacocks (Eurasia, North and South America, 165)
- NUMIDIDAE, Guinea Fowl (Africa, 7)
- MELEAGRIDIDAE, Turkeys (North and Central America, 2)
- OPISTHOCOMIDAE, Hoatzins (South America, 1)

GRUIFORMES, Cranes, Rails, and allies
- MESOENATIDAE, Mesites, Monias (Madagascar, 3)
- TURNICIDAE, Bustard-Quails (Africa, Australia, 15)
- PEDIONOMIDAE, Plain-wanderers (Australia, 1)
- GERANOIDIDAE (fossil)
- EOGRUIDAE (fossil)
- GRUIDAE, Cranes (Africa, Eurasia, North America, 14)
- ARAMIDAE, Limpkins (North and South America, 1)
- PSOPHIIDAE, Trumpeters (South America, 3)
- ORTHOCNEMIDAE (fossil)
- RALLIDAE, Rails, Coots, Gallinules (World-wide, 132)
- HELIORNITHIDAE, Sun-grebes (Tropics, 3)
- RHYNOCHETIDAE, Kagus (East Indies, 1)
- EURYPYGIDAE, Sun-bitterns (Central and South America, 1)
- PHORORHACIDAE (fossil)
- PSILOPTERIDAE (fossil)
- BRONTORNITHIDAE (fossil)
- OPISTHODACTYLIDAE (fossil)
- CUNAMPAIIDAE (fossil)
- BATHORNITHIDAE (fossil)
- HERMOSIORNITHIDAE (fossil)
- CARIAMIDAE, Cariamas (South America, 2)
- OTIDIDAE, Bustards (Eurasia, Africa, 23)

DIATRYMIFORMES
- DIATRYMIDAE (fossil)
- GASTORNITHIDAE (fossil)

CHARADRIIFORMES, Shorebirds, Gulls, Auks
  JACANIDAE, Jacanas (Tropics and Subtropics, 7)
  RHEGMINORNITHIDAE (fossil)
  ROSTRATULIDAE, Painted Snipe (Tropics, 2)
  HAEMATOPODIDAE, Oyster-catchers (World-wide, 6)
  CHARADRIIDAE, Plovers, Turnstones, Surfbirds (World-wide, 63)
  SCOLOPACIDAE, Snipes, Woodcocks, Sandpipers (World-wide, 77)
  RECURVIROSTRIDAE, Avocets, Stilts (World-wide, 7)
  PRESBYORNITHIDAE (fossil)
  PHALAROPODIDAE, Phalaropes (Eurasia, North America, 3)
  DROMADIDAE, Crab-plovers (Africa, Southwest Asia, 1)
  BURHINIDAE, Thick-knees (World-wide except North America, 9)
  GLAREOLIDAE, Coursers, Pratincoles (Africa, Eurasia, 16)
  THINOCORIDAE, Seed-snipe (South America, 4)
  CHIONIDIDAE, Sheath-bills (South Atlantic and Indian Oceans, 2)
  STERCORARIIDAE, Skuas, Jaegers (Subarctic, Subantarctic, 4)
  LARIDAE, Gulls, Terns (World-wide, 82)
  RHYNCOPIDAE, Skimmers (Tropics and Subtropics, 3)
  ALCIDAE, Auks, Auklets, Murres (Eurasia, North America, 22)

COLUMBIFORMES, Pigeons, Doves, Sand-grouse
  PTEROCLIDAE, Sand-grouse (Eurasia, Africa, 16)
  RAPHIDAE, Dodos, Solitaires (Extinct; formerly on Mauritius Rodriguez, and Réunion, 3)
  COLUMBIDAE, Pigeons, Doves

PSITTACIFORMES, Parrots and allies
  PSITTACIDAE, Lories, Parrots, Macaws (Tropics and Subtropics, 315)

CUCULIFORMES, Plantain-eaters, Cuckoos
  MUSOPHAGIDAE, Plantain-eaters (Africa, 19)
  CUCULIDAE, Cuckoos, Road-runners, Anis (World-wide, 127)

STRIGIFORMES, Owls
  PROTOSTRIGIDAE (fossil)
  TYTONIDAE, Barn Owls (World-wide, 11)
  STRIGIDAE, Owls (World-wide, 123)

CAPRIMULGIFORMES, Oil-birds, Goatsuckers
  STEATORNITHIDAE, Oil-birds (South America, 1)
  PODARGIDAE, Frogmouths (Australia, 12)
  NYCTIBIIDAE, Potoos (South and Central America, 5)
  AEGOTHELIDAE, Owlet-frogmouths (Australia, 7)
  CAPRIMULGIDAE, Goatsuckers (World-wide, 67)

APODIFORMES, Swifts, Hummingbirds
  AEGIALORNITHIDAE (fossil)
  APODIDAE, Swifts (World-wide, 76)
  HEMIPROCNIDAE, Crested Swifts (East Indies, 3)
  TROCHILIDAE, Hummingbirds (North and South America, 319)

COLIIFORMES, Colies
  COLLIIDAE, Colis (Africa, 6)

TROGONIFORMES, Trogons
  TROGONIDAE, Trogons (Tropics and Subtropics, 34)

- CORACIIFORMES, Kingfishers and allies
  - ALCEDINIDAE, Kingfishers (World-wide, 87)
  - TODIDAE, Todies (West Indies, 5)
  - MOMOTIDAE, Motmots (Central and South America, 8)
  - MEROPIDAE, Bee-eaters (Africa, Eurasia, 24)
  - CORACIIDAE, Rollers (Africa, Eurasia, Australia, 11)
  - BRACHYPTERACIIDAE, Ground-rollers (Madagascar, 5)
  - LEPTOSOMATIDAE, Cuckoo-rollers (Madagascar, 1)
  - UPUPIDAE, Hoopoes (Africa, Eurasia, 1)
  - PHOENICULIDAE, Wood-hoopoes (Africa, 6)
  - BUCEROTIDAE, Hornbills (Africa, Asia, 45)

- PICIFORMES, Woodpeckers and allies
  - GALBULIDAE, Jacamars (Central and South America, 15)
  - BUCCONIDAE, Puff-birds (Central and South America, 30)
  - CAPITONIDAE, Barbets (Tropics, 72)
  - INDICATORIDAE, Honey-guides (Africa and Southern Asia, 11)
  - RHAMPHASTIDAE, Toucans (Central and South America, 37)
  - PICIDAE, Woodpeckers (World-wide, 224)

- PASSERIFORMES, Perching Birds
  - EURYLAIMIDAE, Broadbills (Africa, Southern Asia, East Indies, 14)
  - DENDROCOLAPTIDAE, Wood-hewers (Central and South America, 63)
  - FURNARIIDAE, Oven-birds (Central and South America, 209)
  - FORMICARIIDAE, Ant-thrushes (Central and South America, 238)
  - CONOPOPHAGIDAE, Ant-pipits (South America, 12)
  - RHINOCRYPTIDAE, Tapaculos (Central and South America, 28)
  - COTINGIDAE, Cotingas (Arizona to South America, 90)
  - PIPRIDAE, Manakins (Central and South America, 59)
  - TYRANNIDAE, Tyrant Flycatchers (North and South America, 365)
  - OXYRUNCIDAE, Sharpbills (Central and South America, 1)
  - PHYTOTOMIDAE, Plant-cutters (South America, 3)
  - PITTIDAE, Pittas (Africa, Asia, Australia, 23)
  - ACANTHISITTIDAE, New Zealand Wrens (New Zealand, 4)
  - PHILEPITTIDAE, False Sun-birds (Madagascar, 2)
  - MENURIDAE, Lyre-birds (Australia, 2)
  - ATRICHORNITHIDAE, Scrub-birds (Australia, 2)
  - ALAUDIDAE, Larks (Africa, Eurasia, North America, 74)
  - PALAEOSPIZIDAE (fossil)
  - HIRUNDINIDAE, Swallows (World-wide, 75)
  - CAMPEPHAGIDAE, Cuckoo-shrikes (Africa, Eurasia, Australia, 58)
  - DICRURIDAE, Drongos (Africa, Southern Asia, Australia, 20)
  - ORIOLIDAE, Old World Orioles (Old World, 32)
  - CORVIDAE, Crows, Magpies, Jays (World-wide, 100)
  - CRACTICIDAE, Bell Magpies (Australia, 13)
  - GRALLINIDAE, Magpie-larks (Australia, 2)
  - PTILONORHYNCHIDAE, Bower-birds (Australia, 17)
  - PARADISEIDAE, Birds of Paradise (Australia, New Guinea, 43)
  - PARADOXORNITHIDAE, Parrot-bills, Suthoras (Asia, 19)
  - PARIDAE, Titmouses (Africa, Eurasia, North America, 65)
  - SITTIDAE, Nuthatches (Eurasia, Australia, North America, 22)
  - HYPOSITTIDAE, Coral-billed Nuthatches (Madagascar, 1)

Certhiidae, Creepers (Old World, North America, 17)
Chamaeidae, Wren-tits (North America, 1)
Timaliidae, Babbling Thrushes (Old World, 261)
Pycnonotidae, Bulbuls (Old World, 109)
Cinclidae, Dippers (Eurasia, North America, 5)
Troglodytidae, Wrens (Eurasia, North and South America, 63)
Mimidae, Thrashers, Mockingbirds (North and South America, 30)
Turdidae, Thrushes (World-wide, 304)
Zeledoniidae, Wren-thrushes (Central America, 1)
Sylviidae, Old World Warblers (Old World, 378)
Regulidae, Kinglets (Eurasia, North America, 20)
Muscicapidae, Old World Flycatchers (Old World, 328)
Prunellidae, Accentors, Hedge-sparrows (Eurasia, 12)
Motacillidae, Wagtails, Pipits (World-wide, 48)
Bombycillidae, Waxwings (Eurasia, North America, 3)
Ptilogonatidae, Silky Flycatchers (Southwestern United States to South America, 4)
Dulidae, Palm-chats (Hispaniola, 1)
Artamidae, Wood-swallows (Africa, Asia, Australia, 10)
Vangidae, Vanga Shrikes (Madagascar, 11)
Laniidae, Shrikes (Old World, South America, 71)
Prionopidae, Wood-shrikes (Africa, Asia, Australia, 13)
Cyclarhidae, Pepper-shrikes (Central and South America, 10)
Vireolaniidae, Shrike-vireos (Central and South America, 3)
Callaeidae, Wattled Crows and allies (New Zealand, 3)
Sturnidae, Starlings (Old World, 103)
Meliphagidae, Honey-eaters (Australia, New Zealand, 160)
Nectariniidae, Sun-birds (Africa, Asia, Australia, 106)
Dicaeidae, Flower-peckers (Africa, Asia, Australia, 54)
Zosteropidae, White-eyes (Africa, Asia, Australia, 80)
Verionidae, Vireos (North and South America, 41)
Coerebidae, Honey-creepers (Florida to South America, 36)
Drepanidiidae, Hawaiian Honey-creepers (Hawaii, 22)
Parulidae, New World Warblers (North and South America, 109)
Ploceidae, Weaver-birds (Africa, Eurasia, Australia, 263)
Icteridae, Blackbirds, Troupials (North and South America, 88)
Tersinidae, Swallow-tanagers (South America, 1)
Thraupidae, Tanagers (North and South America, 197)
Catamblyrhynchidae, Plush-capped Finches (South America, 1)
Fringillidae, Grosbeaks, Finches, Buntings (World-wide except Australia, 426)

Appendix III

Official State Birds

All the forty-eight states and the District of Columbia have "designated" state birds, which evidences further the appeal that birds have to people. Only Saskatchewan among the Canadian provinces has adopted a bird (Sharp-tailed Grouse), though the legendary Thunder-bird made famous by Indian stories, and appearing frequently in the totem art of the Coast Indians (see Fig. 22.2d), is a sort of unofficial provincial emblem of British Columbia. It has been adopted, moreover, as the emblem of the University of British Columbia. Mexico uses the Caracara (Mexican Eagle) as its emblem, and the United States the Bald Eagle. In the case of a few birds or states, some confusion ensues because of different ways by which birds may have been "designated":

Alabama	Yellow-shafted Flicker
Arizona	Cactus Wren
Arkansas	Mockingbird
California	Valley Quail
Connecticut	Rose-breasted Grosbeak
Delaware	Cardinal
District of Columbia	Wood Thrush
Florida	Mockingbird
Georgia	Brown Thrasher
Idaho	Mountain Bluebird
Illinois	Cardinal
Indiana	Cardinal
Iowa	Goldfinch
Kansas	Western Meadowlark
Kentucky	Cardinal
Louisiana	Brown Pelican
Maine	Black-capped Chickadee
Maryland	Baltimore Oriole
Massachusetts	Veery
Michigan	American Robin

Minnesota	Eastern Goldfinch
Mississippi	Mockingbird
Missouri	Eastern Bluebird
Montana	Western Meadowlark
Nebraska	Western Meadowlark
Nevada	Mountain Bluebird
New Hampshire	Purple Finch
New Jersey	Eastern Goldfinch
New Mexico	Road-runner
New York	Eastern Bluebird
North Carolina	Carolina Chickadee
North Dakota	Western Meadowlark
Ohio	House Wren
Oklahoma	Bob-white
Oregon	Western Meadowlark
Pennsylvania	Ruffed Grouse
Rhode Island	Bob-white
South Carolina	Carolina Wren
South Dakota	Western Meadowlark
Tennessee	Mockingbird
Texas	Mockingbird
Utah	Gull
Vermont	Hermit Thrush
Virginia	American Robin
Washington	Goldfinch
West Virginia	Eastern Cardinal
Wisconsin	American Robin
Wyoming	Western Meadowlark

Appendix IV

Glossary

ACCIDENTAL SPREAD. Distribution of a bird by some unusual means, such as by hurricanes.

ACTIVITY RANGE. The area over which a bird regularly carries on its affairs.

ADVENTITIOUS COLOR. A color caused by chemical or other coloring agents of the habitat.

AEROBIC. Oxidation in the presence of free oxygen.

AFTERSHAFT. A smaller feather attached to the underside of a contour or other feather.

AGE CLASS. The division of a population into birds of different ages.

AGE OF MATURITY. Age at sexual maturity; sometimes may be used to mean age of fully adult plumage.

AIR SACS. Sacs attached to the respiratory system of a bird for ventilating the interior of the body.

AIR SPEED. Speed with respect to air in which a bird flies.

AIRFOIL. Shape of the wing in cross section; sometimes the same as wing.

ALBINISM. Absence of the normal color and replacement with white, either partially or completely.

ALLANTOIS. An embryonic membrane for respiration and excretion.

ALLELOMORPH. Alternate forms of a gene or inherited character; same as allele.

ALLEN RULE. Projecting body parts become reduced in warm-blooded animals in the colder regions.

ALLOPATRIC SPECIES. Species rather identical in appearance and habits whose ranges geographically complement each other.

ALTRICIAL. Young hatched in a helpless state.

ALULA. The thumb of birds and feathers attached to it; serves as a wing slot in flying.

ANAEROBIC. Oxidation in the absence of free oxygen.

ANEMOMETER. A wind gauge.

ANGLE OF ATTACK. The angle of the wing relative to the air stream.

ANTIBODY. A protective substance produced in the body to neutralize a foreign protein.

AORTA. A large artery, usually one connected to the heart.

APTERIA. The bare space between feather tracts.

APTOSOCHROMATISM. A moltless change of color or pattern, usually by breaking off of feather tips of overlying feathers to expose those underneath; also called aptosochroism.

Arboreal. Tree climbing, dwelling, or living habit.
Archosauria. A subclass of reptiles, including the dinosaurs; common name is Ruling Reptiles.
Arpeggio. Tones of a chord heard in ascending or descending succession.
Aspect Ratio. Ratio of length to width of the wing.
Association. (1) The flocking together or associating of birds by choice; (2) a cover type in ecology.
Associational Barrier. A barrier to spread because of unfavorable environment.
Auricle. The part of the heart receiving blood.
Austral. Southern.
Autosome. A chromosome other than a sex chromosome.
Average Age. The arithmetic mean age of a population or group as a whole.
Averill Rule. The more migratory birds lay eggs of greater length-breadth ratio.

Back Cross. Mating with an individual of parent genotype.
Barograph. An air pressure recorder.
Barrier. An external factor preventing distribution.
Basisphenoid. A bone of the skull.
Bergmann Rule. Warm-blooded animals tend to be larger in the colder parts of the range.
Biochromes. Animal pigments.
Biomass. (a) The amount of animal life in an area by weight; (b) the animals of an area being studied by weight; (c) a group of animals considered according to weight.
Biome. A major vegetation region; sometimes includes animals.
Biotic Province. Named regions or areas of similar topography, climate, plant, and animal life.
Boreal. Northern; may be used sometimes to mean Arctic or Subarctic.
Bowman's Capsule. The part of the nephron surrounding the glomerulus.
Brachial Plexus. A network of connections of nerves of the wings.
Branchial Arch. A gill arch.
Breeding Potential. The theoretical rate at which a species could breed if all eggs and offspring succeeded.
Bursa of Fabricius. A pocket in the cloaca; it may be useful for telling age in some birds.

Caecum. A saclike structure on the intestine.
Calamus. The inner end of a feather shaft.
Camber. Relative curvature of an airfoil.
Carotenoids. Red, orange, or yellow pigments of carotene origin.
Carpal. A bone of the wrist.
Carrying Capacity. The number of birds that the environment can support, particularly with reference to the pinch period.
Cervical Plexus. A network of connecting nerves of neck region.
Chalaza. A ropelike structure at the ends of yolk.
Chord. Three or more related tones sounded together.
Chromosome. Rodlike bodies in the cell nucleus that carry genes.
Clavicles. Collar bones; also called wishbone, furcula.
Climax. The type of vegetation maintaining itself under the existing climate.

Climograph. A graph comparing rainfall and temperature or other climatic elements for different areas.

Cline. A taxonomic series, usually a gradual transition of character between two extremes.

Cloaca. The cavity into which the digestive, excretory, and reproductive systems empty.

Coccidiosis. A disease caused by *Coccidia.*

Cochlea. A part of the inner ear.

Columella. A bone of the inner ear.

Combined Density. The density of two species without adjustment for any overlap in life requirements.

Commensalism. An association of species in which one is benefited and the other not harmed.

Community. A group of organisms together with their environment.

Compensatory Adjustment. (a) Variation in the number of individuals to meet seasonal or other environmental changes; (b) variation in the combined density because of overlapping requirements.

Cones. Structures of the retina concerned with color perception.

Congregation. A grouping of birds because of environment, as at a feeding area.

Convergence. The similarity of two species because of life habits rather than relationship.

Coracoids. Bones of the pectoral girdle that brace the sternum to the shoulders.

Corascoscapular-humeral. Jointly referring to coracoid, scapular, and humerus.

Coriolis Force. *See* Deflection.

Corpus Callosum. A large band of nerve fiber joining brain hemispheres.

Corpus Striatum. A structure of the brain forward of the thalamus.

Cotylosauria. An order of Permian reptiles; commonly called Stem Reptiles.

Cover. The vegetation of a bird's environment; may sometimes refer to nonliving items such as "escape cover" in the form of rocks or brush piles.

Cover Type. Designation of cover by name of conspicuous plants.

Covey. A flock, as of Quail.

Cursorial. A running habit of life.

Deferred Maturity. One sex reaching maturity in a different year from the other.

Deflection. The tendency of moving objects to turn to the right in the Northern Hemisphere and to the left in the Southern Hemisphere because of the earth's rotation.

Density. The number of birds relative to area.

Density Relations. Conditions governed by the number of birds are called "density dependent"; those not so related are called "density independent."

Detection Distance. In field studies, the distance from the observer to a bird at the moment of its sighting.

Diapsid Skull. Having two lateral fossas.

Diatonic Scale. Seven-toned major and minor scales, such as C D E F G A B.

Dichromatism. The appearance of a species in more than one coloration; sexual dichromatism means different colors for male and female; a color phase is a normal kind of dichromatism.

Diel. Referring to the 24-hour day; same as daily when so used (but daily can mean only the daylight part of the 24-hour day).

Diencephalon. The " 'tween brain."

Differential Mortality. Different death rates, as for the two sexes or adult and young.

Displacement Action. A substitute activity, such as an attack on some alien object by a bird when an intruder is at the nest.

Diurnal. Referring to the daylight part of the day.

Diurnal Migration. Migration regularly in the daytime rather than at night as by many Hawks, Geese, or Blackbirds; may refer to any migration in daylight.

Dominance. The relationship between individuals in a flock or other group in which one becomes socially superior to the other, the latter socially inferior to the former.

Dominant. In genetics, a character that dominates over the recessive.

Dorsal. Referring to the back or upper part; toward the back.

Drag. Resistance of air to the body in flight.

Drumming. Production of sounds by beating the wings, as in the Ruffed Grouse; may also refer to other instrumental sounds, such as beating of a tattoo with the bill, as in Woodpeckers.

Duodenum. The fore part of the intestine.

D-v-p System. The type of air circulation in bird lungs.

Eclipse Plumage. A transitory post-breeding season plumage of some ducks.

Ecological Homologues. Birds of analogous ecological needs in widely separated regions.

Ecological Succession. The orderly transition of an area through definite ecological stages.

Ecology. The study of the relations of an organism and its environment.

Ecotone. An edge, particularly between ecological types.

Ectoderm. The outer embryonic layer.

Ectoparasite. A parasite inhabiting the surface of the body.

Edaphic. Conditions not in harmony with climatic expectation owing to soil.

Edge Effect. The tendency of birds and other animals to be more numerous at the boundaries of ecological types than in the interior.

Efferent Duct. A tube leading from an organ or other structure.

Egg-Success Expectancy. Ratio of number of eggs produced to parents.

Egg-Success Ratio. Number of eggs laid in relation to number of young produced.

Endemic. Native in its evolutionary home.

Endoderm. The innermost embryonic layer.

Endolymph. Fluid of the ear labyrinth.

Environmental Resistance. The adverse influence of the environment upon survival.

Enzyme. An organic ferment or catalyst of the body.

Epididymis. The efferent tubules of the testis.

Erythrocyte. A red blood corpuscle.

Erythroism. An excess of red plumage.

Esophagus. The tube connecting mouth and stomach.

Estrogen. An ovarian endocrine.

Ethmoid. A bone in the floor of the skull.

EUSTACHIAN TUBE. A tube connecting the inner ear with the mouth to equalize air pressure on two sides of the ear membrane.

EVOLUTIONARY SUCCESSION. The gradual replacement of one species or group with another in the past; probably continuing in the present.

EXTINCTION THRESHOLD. The minimum abundance to which a species could be reduced beyond which it must become extinct.

EXTRINSIC MUSCLES. External muscles of the syrinx.

FAHRENHOLZ RULE. A close relationship of parasites indicates close relationship of hosts.

FALL RECRUDESCENCE. The reappearance of characteristics of the breeding season in the fall, such as drumming by Ruffed Grouse.

FAMILY. A taxonomic unit of related genera.

FEATHER TRACT. The rows or bands in which feathers grow.

FEMUR. Thigh bone.

FERAE NATURAE. A legal term meaning wild animals in contrast to domesticated ones.

FIBRINOGEN. A blood structure.

FILOPLUMES. Hair-like feathers at the base of outer feathers.

FIXED INTONATION. The pitch of a note fixed mechanically as in the piano; equal temperament scale.

FLAT. (a) A musical sign that lowers a note by a half step; (b) a note sung lower than the intended or correct one.

FLEDGLING. A young bird fully feathered but still in the nest.

FLIGHT, FLIGHT YEAR. The invasions of northern birds to more southerly regions after a period of absence or presence in small numbers; sometimes used for other invasions; also used for migration, as of water birds.

FLIGHT SPEED. Usually flight speed means speed with respect to the ground; sometimes used for air speed.

FLOCK RANGE. The area over which a flock wanders, usually in winter.

FLUSHING DISTANCE. A detection distance based upon scaring up (flushing) a bird, especially Ruffed Grouse.

FOOD CHAIN. The several steps in an energy-transfer system among plants and animals.

FOOD WEB. The several related food chains of an environment.

FORM. Sometimes used as a synonym for subspecies, race, or other taxonomic variation.

FREEZE. A young bird or other animal that becomes motionless when disturbed or when danger threatens is said to "freeze."

FURCULA. Wishbone.

FREQUENCY. (a) The number of vibrations per second in music; (b) relative occurrence in counts or censuses.

GALLINACEOUS. Referring to members of the order Galliformes.

GENE. Unit of inheritance.

GENERALIZATION. A summary or conclusion relative to the common characteristics of whatever has been studied. (A *postulate* is a low order of conclusion. A *hypothesis* is deemed more substantial than a postulate. A *theory* is more substantial than a hypothesis but not proved enough to constitute an established principle. *Rule*, *principle*, and *law* are used interchangeably for generalizations deemed established as valid. *Law* usually connotes a principle of highest substance and validity.)

GENETICS. The study of inheritance.
GENOTYPE. Genetic make-up.
GENUS. A taxonomic unit of one or more closely related species.
GEOGRAPHIC COMPLEMENT. Related species that replace each other geographically; one declines as the other increases.
GIZZARD. The grinding organ of the stomach.
GLOGER RULE. Animals of humid regions tend to be darker, those of dry lands lighter in color.
GLOMERULUS. The group of capillaries in a renal capsule.
GONAD. Ovary or testis.
GONADOTROPINS. A hormone acting upon ovary or testis.
GRAVIPORTAL. Ponderous animals like the Elephant Bird.
GROUND SPEED. Flight speed with respect to the ground.
GUANO. Excrement of birds, especially Cormorants, that accumulates in dry regions; applied to accumulations of excrement of other birds and bats also.

HABITAT. The place occupied by an animal; of analogous use to site for plants.
HAMULUS. Hooklet on a barbicel.
HARMONIC INTERVAL. Two related tones sounded together.
HARMONY. A combination of related tones.
HEMOGLOBIN. The part of the blood that carries oxygen.
HEPATIC PORTAL SYSTEM. Veins connecting the digestive tract and liver.
HESPERORNIS. A toothed Cretaceous bird from Kansas.
HETEROGAMETIC. Gametes with more than one kind of sex chromosome; in birds, the female is the heterogametic sex and produces ova having chromosomes for male and female.
HETEROZYGOUS. Having one gene of a pair the dominant, the other the recessive.
HIBERNATION. The torpid condition for passing cold periods.
HIPPOBOSCID FLY. A parasitic fly.
HOLARCTIC. A term used for Palearctic and Nearctic combined.
HOME RANGE. The area which a bird regularly inhabits.
HOMOGAMETIC. Producing gametes with sex chromosomes all alike; the male is the homogametic sex in birds.
HOMOIOTHERMOUS. A body temperature remaining constant regardless of environmental temperature; commonly called "warm-blooded."
HOMOZYGOUS. Having both genes of a pair either recessive or dominant.
HORMONE. A secretion of an endocrine gland distributed by the blood stream; same as endocrine.
HUMAL BARRIER. A barrier to distribution because of humidity.
HUMERUS. The upper wing bone.
HYALINE. A type of cartilage.
HYBRID. A cross between two species; sometimes used for a cross between two races or a cross between two breeds.
HYDROSERE. Succession in a water environment.
HYGROGRAPH. An instrument for recording humidity.
HYOID. The second visceral arch; supports the tongue in birds.
HYPOPHYSIS. The pituitary gland.
HYPOTHESIS. *See* Generalization.

ICHTHYORNIS. A Cretaceous fossil.
ILIUM. A bone of the pelvic girdle.

IMMATURE. A young bird in first winter plumage.

IMPRINTING. Learning by a very young bird; often used for alien habits acquired in place of normal ones.

INSERTION. The movable end of a muscle.

INTERNAL ADJUSTMENT FACTORS. Variations in breeding potential from geographic, density, age, or other influences upon breeding.

INTERNAL METAMERISM. Internal body divisions, especially as in fish.

INTERPREDATION. Predator preying upon another predator.

INTERSPERSION. Ecological mixing.

INTERSTITIAL CELLS. Endocrine cells of gonads.

INTERVAL. The difference in pitch between two tones.

INTRATARSAL. The ankle joint between tarsal bones.

INTRINSIC MUSCLES. Muscles within the syrinx.

INVERSITY. The tendency for breeding to be high when the population is low and low when the population is high.

ISCHIUM. A bone of the pelvic girdle.

ISOLATION. The separation of groups by which taxonomic differences may arise.

JUST INTONATION. The untempered or natural scale.

JUVENAL. A variant spelling of juvenile.

JUVENILE. A young bird out of nest but not yet having completed post-juvenile molt.

KEEL. The knifelike ridge of a bone, especially that of the sternum, for greater muscle attachment.

KYMOGRAPH. A drum recorder.

LAMBERT'S LAW. The relationship of heat loss and body shape.

LARYNX. The voice box of mammals; located at the upper end of the trachea.

LAW. *See* Generalization.

LEUCOCYTES. White blood corpuscles.

LIFE EQUATION. Gain in the number of birds at the breeding season equals losses throughout the year.

LIFE EXPECTANCY. Average life to be expected on basis of date chosen for reckoning.

LIFT. Upward component of pressure on the wings.

LIMIT OF TREES. The poleward edge of tree distribution.

LIMITING FACTOR. The most restrictive at the moment of the many factors of environmental resistance.

LINK. An energy transfer step in a food chain.

LINKAGE. Genes carried by the same chromosome.

LONGEVITY. Actual length of life of an individual.

LUMBOSACRAL PLEXUS. A network of connecting nerves in the pelvic region.

MACROCLIMATE. The climate of a region or other large area.

MAJOR SCALE. A particular succession of whole and half tones that produces a happy or positive effect on the hearer.

MAJOR SECOND. The interval between *do* and *re* of the major scale.

MAJOR THIRD. The interval between *do* and *mi* of the major scale.

MALLOPHAGA. An order of insects parasitic on birds.

MANDIBLE. The lower jaw.

MANIFEST CURVE. A graph of a time series having rhythmic, nonrhythmic, and random data.

MARGINAL HABITAT. Environment barely suited to the needs of a species.

MAXIMUM AGE. The age to which the body might live.

MELANIN. The dark pigment of feathers or skin; in concentration it looks black though actually it is a dark-brown pigment.

MELANISM. An excess of dark pigment; a normal dark phase, as in some Hawks, is called a melanistic phase rather than melanism.

MELODIC INTERVAL. Two related tones sung successively.

MELODY. A series of related musical tones arranged to produce a distinct musical phrase or idea.

MEROBLASTIC DISCOIDAL CLEAVAGE. Cleavage involving only part of the egg, as in the bird.

MESENCEPHALON. A division of the brain forward of the metencephalon.

MESODERM. The middle embryonic layer.

MESOTARSAL. The ankle joint between tarsal bones; also called intratarsal.

METABOLISM. The sum of life processes, mostly chemical, in the body.

METACARPALS. Bones of the wrist.

METANEPHRIC KIDNEY. The type of kidney found in reptiles, birds, and mammals.

METENCEPHALON. A division of the brain, forward of the mylencephalon.

MICROCLIMATE. A localized climate, such as under a tree, in the open, on different exposures of slopes.

MICROTONE. An interval smaller than a semitone.

MINOR SCALE. A particular stepwise succession of whole and semitones that produces a mournful or negative effect on the hearer.

MINOR SECOND. A major second interval reduced chromatically by a half step.

MINOR THIRD. A major third interval reduced chromatically by a half step.

MITOTIC RATE. The rate at which mitosis or cell division takes place; tends to be the opposite of the activity rate.

MIXED DENSITY. The density of two species with overlapping environmental use; hence, the combined density adjusted for overlap.

MOLT MIGRATION. A movement of waterfowl to secluded marshes for the post-breeding molt.

MONOGAMY. One male mated to one female only (and vice versa).

MORTALITY RATE. Death rate.

MOSASAUR. Mesozoic reptiles of suborder Sauria.

MUTUALISM. A relationship between organisms by which one or both benefit.

MUTATION. Sudden changes of gene pattern that are inherited.

MYLENCEPHALON. Medulla oblongata.

MYOLOGY. The study of muscles.

NATIVE. Living in an area to which it spread naturally rather than artificially in the wake of man.

NEARCTIC. North America north of Central America.

NEOSSOPTILES. Down of the young bird.

NEOTROPICAL. South and Central America.

NESTLING. A young bird not yet ready to leave nest.

NEUTRAL GROUND. An area in which birds may be active but which they do not claim as part of their territories.

Niche. The particular ecological combination that a species uses; sometimes synonymous with life form.

Nictitating Membrane. The third eyelid in birds.

Nocturnal. Referring to night time.

Nocturnal Migration. Migration by night, as in many Passerines.

Nomadism. A vagrant type of life, as in Crossbills.

Notochord. The axial support in chordate embryos.

Obligate Parasite. A parasite that lives on a single species only.

Oblique Septum. A partition in the abdominal region.

Occipital Condyle. The rounded projection of the occipital bone on which the skull articulates with the vertebral column.

Oil Droplets. The cones of the retina usually have droplets (orange, red, yellow) to aid color vision.

Oogenesis. Development of the ovum.

Orbit. Eye socket; sometimes used to mean eye.

Origin. The fixed end of a muscle; attachment to bone.

Ornithischia. Order of Mesozoic Ruling Reptiles.

Ornithophillus. Pollination by birds.

Orthogenesis. The theory that evolution may move along some lines because of some internal direction.

Osmosis. Diffusion through a semipermeable membrane.

Ovary. Female gonad.

Overtone. Harmonics of a fundamental.

Oviduct. The tube along which the egg moves.

Oxygen Debt. Use of oxygen stored chemically.

Oxyhemoglobin. Hemoglobin combined with oxygen.

Palatine. Bone of the skull.

Palearctic. Old World north of Sahara and Himalayas.

Pancreas. A gland producing digestive fluids; contains Isles of Langerhans that produce insulin.

Papilla. A small bump in the skin or other surface.

Passerine. A bird of the order Passeriformes.

Peck Dominance. The dominance of one bird over another in most of their contacts.

Peck Order. The rank of the several members of a social hierarchy; arrangement according to dominance.

Pecten. A structure in the eye; many theories have been proposed for its function—one is that it aids in sun or star navigation.

Pectoral Girdle. Bones of the shoulder and breast region.

Pelagic. Wandering over the oceans, especially parts remote from land.

Pelvic Girdle. Bones of the hip region.

Pentatonic. A five-toned scale; common in primitive music.

Peripheral Intolerance. The habit of birds to occupy only the choicest habitat near the limits of their ranges.

Permanent Resident. A bird that lives in the same region the year around; a nonmigratory bird.

Pessulus. Part of the syrinx covered by the vibratory semilunar membrane.

Phalanges. Bones of the finger or toe.

Pharyngeal Gills. Gills located in the pharynx.

PHARYNX. The region between mouth and esophagus.

PHENOLOGY. Study of the succession or progress of the season.

PHENOTYPE. Body make-up.

PHOTOPERIOD. Amount of daylight; alternation of day and night.

PHOTOSYNTHESIS. Chemical action by plants in the presence of light.

PHRASE. A short series of related musical notes, usually three to five measures long.

PHYLOGENY. The racial history of a species or group.

PINCH PERIOD. The severest part of the year from the standpoint of survival, usually the winter.

PITCH. A characteristic of a sound that depends upon the number of vibrations per second.

PLATELETS. Blood structures in mammals; similar to thrombocytes.

PLUMULES. Down of the adult.

POIKILOTHERMOUS. Body temperature varying with that of the environment; commonly called "cold-blooded."

POLYGAMOUS. Mating of one male with more than one female. (*Polyandry* is the mating of one female with more than one male. *Polygyny* refers to either polygamy or polyandry.)

POLYLECITHAL. Eggs heavily loaded with yolk, as in birds and reptiles.

POPULATION RESERVOIR. Birds without mates or territories during the breeding season.

PORPHYRIN. Reddish colors of hemoglobin origin.

POSTULATE. *See* Generalization.

POTENTIOMETER. A recorder that operates on differences in electrical potential.

POWDER DOWN. A special bunch of feathers which breaks up into a powder that serves as a dry shampoo in some birds.

PRECOCIAL. Young that can partially care for themselves, as in Grouse or Ducks.

PRIMARY. A main flight feather.

PRIMARY SEX RATIO. Sex ratio at the time of fertilization.

PRINCIPLE. *See* Generalization.

PROLACTIN. A hormone of the pituitary.

PROMISCUITY. Copulation without forming a mating bond.

PROVENTRICULUS. The fore part of the stomach.

PTEROSAURIA. An order of extinct, flying reptiles.

PTERYGOID. A bone of the skull.

PTERYLA. A feather tract.

PTERYLOGRAPHY. Feather arrangement.

PTERYLOSIS. Feather arrangement.

PTILOSIS. Feather arrangement.

PURE TONE. A tone having no overtones; a tone of but one wave length.

PYGOSTYLE. Tail bone, sometimes called "plowshare bone"; with the fleshy part of the tail, sometimes called "the Pope's nose."

PYLORIC MUSCLES. Muscles controlling the outlet from the gizzard.

PYRAMID OF NUMBERS. A table listing the animals of an area on the basis of most numerous to least numerous.

QUADRAT. A sample plot, originally square.

QUADRATE. A bone of the skull.

QUALITY. Variations giving bird sounds their individual character.

RACE. Sometimes used as a synonym for subspecies or other geographic variation.

RACHIS. The outer part of a feather shaft.

RADIUS. Smaller bone in the forewing.

RANGE. Range may mean (a) geographic area occupied by a species; (b) area over which an individual or flock moves; or (c) the habitat of a species.

RANGE COMPLEX. The composite conditions of the bird and environment that determine occupation and size of range.

RAPTORIAL. Predatory birds, specifically those of the order Falconiformes; sometimes called *raptoral.*

RAYLEIGH EFFECT. The scattering of light rays in the atmosphere.

RECESSIVE. Subordinate to dominant characters in genetics.

RECRUDESCENCE. A resurgence after a period of quiet, as of drumming in the fall by Ruffed Grouse.

RECTRIX. The main tail feather.

REFRACTORY PERIOD. The period of reduced size of gonads with decline of breeding.

RELEASER. An action or other factor that causes a response.

RELICT SPECIES. Species of restricted range that formerly were widely distributed.

RENAL PORTAL SYSTEM. The capillaries and veins that return blood to the heart via the caudal and renal veins.

RODS. Slender receptors of the retina concerned with light perception.

RULE. *See* Generalization.

RULING REPTILES. The common name of Mesozoic Reptiles of subclass Archosauria.

RUPTIVE PATTERN. Bold streaks and blotches that break up the outline of an object; also called disruptive patterns.

SACCULUS. Part of the inner ear.

SACRAL VERTEBRA. Vertebra associated with the hip.

SAMPLE COUNT. Enumeration of a representative part of a population.

SATURATION POINT. The maximum density under which a species will normally live.

SCANSORIAL. Climbing habit of life.

SCLEROTIC RING. A ring of bony plates surrounding the eye.

SECONDARIES. Inner flight feathers.

SECONDARY SEX RATIO. The sex ratio at hatching.

SECULAR. Nonrandom and nonrhythmic changes with time.

SEMANTIC COLOR. A signal color, such as white in the tail of the Meadowlark.

SEMILUNAR MEMBRANE. A membrane covering the pessulus in the syrinx; the vibratory membrane of the syrinx.

SEMINIFEROUS TUBULE. A sperm tubule of the testis.

SEMIPLUMES. Adult feathers similar to outside feathers but lacking interlocking devices.

SEPTUM. A wall or partition.

SEQUESTRATION NOTES. Calls designed or used to keep others of a flock from coming too close.

SEX-LINKED CHARACTERS. Characters whose genes are carried by sex chromosomes.

SEXUAL DICHROMATISM. The male and female of different colors, as in the Mallard Duck.

SEXUAL DIMORPHISM. The male and female of different body form; in birds, it is used to mean marked difference in body size, as in the Sage Grouse.

SHARP. (a) The musical sign that raises a note by a semitone; (b) singing that rises above the intended or correct note.

SIBLING. A term meaning either brother or sister; species like the Hairy and Downy Woodpeckers are sometimes called "sibling species."

SIGMOID. An S-shaped curve.

SNOW LINE. The lower limit of permanent snow or ice in mountains.

SOCIAL HIERARCHY. The social order of birds in a group.

SOCIAL PARASITISM. Laying eggs in the nest of another bird, as in the Old World Cuckoo.

SPECIES. A population of birds reproductively isolated.

SPERMATOGENESIS. Development of the sperm.

SPERMATOZOAN. Functional sex cells of the male.

SPREAD WAY. A route over which a species invades new range.

STAGE. A step in ecological succession.

STEM REPTILES. The common name for reptiles of the Permian order Cotylosauria.

STERNUM. Breast bone.

SUBSPECIES. A named variation within a species.

SUMMER RESIDENT. A migrant bird found in summer only.

SUPPORT DIFFERENCES. Differences in capacity of an area or cover type to provide living needs of birds.

SYMBIOSIS. A relationship between two organisms such that both benefit.

SYMPATRIC SPECIES. Species practically alike in looks, habits, and range, but which do not interbreed.

SYRINX. The voice box of the bird; located at the lower end of the trachea.

TARSAL. Referring to tarsus or ankle; in birds, the term commonly means the same as tarsometatarsal.

TAXONOMY. Study of classification and naming.

TELENCEPHALON. The front division of the brain.

TELEOPTILES. Feathers of the adult.

TELOLECITHAL. Having the yolk concentrated in one part of the egg.

TEMPERED SCALE. A compromise of tuning, as on the piano or other instrument of fixed pitch.

TERRITORY. The defended part of the range.

TERTIARY SEX RATIO. The sex ratio of adults.

TESTOSTERONE. Male sex hormone.

TETRAPYRROLES. Colors of hemoglobin or bile origin; usually reddish or brownish but may include blue or bluish green, as in some egg-shell colors.

TETRARADIATE PELVIS. A pelvis of four divisions.

THECODONT. A Mesozoic reptile of the order Thecodontia.

THEME. A musical idea or musical subject.

THEORY. *See* Generalization.

THERMAL. A column of air rising over a heated surface.

THERMOCOUPLE. A bimetallic device for recording temperature changes by electrical impulses induced by differences between the metals.

THERMOGRAPH. A recording thermometer.

THERMONEUTRAL. The temperature at which a warm-blooded animal in effect feels neither hot nor cold.

THERMOTAXIC NERVE. The part of the nervous system regulating body temperature.

THYROXIN. A hormone produced by the thyroid gland.

TIBIOTARSUS. The fused tibia and tarsal bones in birds.

TOLERANCE. The capacity of birds to withstand or adjust to disturbed conditions in the environment; said also of the capacity to use widely differing habitats.

TOTIPALMATE. All four toes webbed.

TRACHEA. Windpipe.

TRADITION. The habits of birds learned by association with others as distinguished from individually learned habits or instinctive ones.

TRANSECT. A line along which birds are counted.

TRANSIENT. Migrant.

TRANSMUTATION. An ancient belief that a bird found only in winter became transformed into another found only in summer and vice versa.

TREE LINE. The limit of trees in mountain regions.

TURACIN. A red pigment containing copper found in certain Musophagidae.

TUROCOVERDIN. A green pigment found in certain Musophagidae.

TYMPANIC MEMBRANE. The vibratory membrane of the ear.

TYPE. In taxonomy, the specimen upon which a taxonomic name is based; called also type specimen; the type locality is the place where type was found. *See also* Cover Type.

ULNA. The larger bone of the forewing.

UNCINATE PROCESS. A hook-shaped projection on the rib.

UNGULATE. Cattle-like mammals.

UROPYGIAL GLAND. The oil gland in the tail.

UTRICULUS. A compartment of the inner ear.

VAGRANT MIGRATION. Post-breeding season wanderings of young birds; sometimes refers to other wandering of birds.

VAS DEFERENS. A duct leading from the testis.

VESTIGIAL BEHAVIOR. An act performed by a bird that resembles an act of a distant relative but which seems no longer functional in the former.

VITELLINE MEMBRANE. The membrane surrounding the yolk.

WATTLE. Fleshy structures on the heads of Chickens.

WING FLASHING. The habit of some birds, especially the Mockingbird, of raising and lowering the outstretched wings when feeding.

WING LOAD. Weight relative to wing area.

WINNOWING. Aerial performance of a Snipe during which a special sound is made.

WINTER RESIDENT. A migrant bird found in a region only in winter.

XANTHROCHROISM. An excess of yellow in the plumage.

XEROSERE. Succession in dry environment.

ZYGODACTYLY. "Yolk-toed" condition, as in the Kingfisher.

Index

Abundance, 244–250; relative, 246; relative and absolute, 468–469
Accipitriidae, 152, 239, 282
Adaptability to changed environment, 186–189
Adaptations: aspects of life, 149; environment, 35–37; evolution, 149–150; foot, 46–48; flight, 20–22; forelimb, 37–39; head, 42–46; swimming, 47; tail, 39–42
Adaptive characters, 34
Adaptive nature of music, 320
Adaptive radiation, 163–165, 166
Adaptiveness and survival, 149
Adjutant (*Leptoptilus*), 276
Adrenal, 64, 72
Aerodynamics of flight, 272–278
Age: average, 134; breeding, 135; captives, 13, 136; maturity, 125; maximum, 134; seasonal changes, 138–139
Age and population, 136–146
Age composition, 136–138
Age counts, 138–139
Age factors, 134–136
Age indicators, 139–140
Air sacs, 21, 23, 65, 66, 67
Airfoil, 271, 272, 273
Alaska-Siberia land bridge, 172, 175, 196
Albatross, 16, 38, 218; distribution, 171; habits, 203; migration, 292; nestling, 386; plumage, 417; temperature, 83
Albinism, 125, 396
Allen Rule, 80, 185, 186
Alligator, 7
Allopatric species, 26, 191–192
Altitude, 215–216; relation to latitude, 183–185, 216
Alula, 38, 55; function, 273
Amateurs, role of, 458
American Ornithologists' Union, 30, 416
Anatomy, 15, 49–60
Ancestry of birds, 6–10
Anhimidae, 195
Anhinga, 67, 193
Ani (*Crotophaga*), 348; egg color, 102; territory, 221
Ankle joint, 19, 56–57
Anseriformes, Pleistocene, 152; flocks, 239; incubation, 110
Ant-thrush (Formicaridae), 195, 321
Anting, 242–243
Aortic arch, 18
Aptosochroism (aptosochromatism), 123–124
Aquatic adaptation, 16, 36
Archaeopteryx (*Archaeornis*), 7, 8, 10–12, 33, 40
Archosaurs, 6, 7, 10
Arkansas, 332, 421
Association (flocks), 238
Attracting birds, 427–431
Auk, Great (*Plautus impennis*), 162, 163, 354; extinction, 419, 453; migration, 297
Auk, The, 419
Auklet, Rhinoceros (*Cerorhinca monocerata*), 44
Averill Rule, 104, 186
Avocet (*Recurvirostra*), 83, 355

Baldpate (*Mareca*), 146, 283
Banding, 469–471
Barriers, 173–175
Bathing, 409–410
Bats (Chiroptera), 36, 271, 282
Becard, Rose-throated (*Platypsaris aglaiae*), 363
Bee-eater, Rosy (*Merops*), 241
Behavior evolution, 152–153
Bell-bird (*Procnias*), 46
Bergmann Rule, 185, 186, 397, 436; heat production, 84–85
Bill adaptations, 42–44; adornments, 44; muscles, 53–54
Binoculars, 463–465
Binomial system, 30

Biogeographic divisions, 177–180
Biogeographic factors of distribution, 177–189
Biological energy, 198–199, 320; competition, 199; entrapment, 207; food chain, 443–444
Biomass, 149, 210, 256–257
Biomes, 179, 204
Biotic provinces, 179
Bird flight, 266–288
Bird houses, 428, 430
Bird of Paradise (Paradiseidae), 39; color, 123; display, 353; song, 350
Bird song, 319–345
Bird's nest soup, 61
Bishop, Red (*Euplectus orix*), 229
Bishop Bird, Crimson-crowned (*Euplectus hordeacea*), 348
Bittern (*Botaurus*), 128, 200, 384
Bittern, Least (*Ixobrychus exilis*), 243
Blackbird, Brewer (*Euphagus cyanocephalus*), 394
Blackbird, English (*Turdus merula*): age, 136; age ratio, 138; food, 436; life expectancy, 139; sex ratio, 146; territory, 227
Blackbird, Red-winged (*Agelaius phoeniceus*), 39, 165, 166, 200; abundance, 261; age, 142, 145; albinism, 125; arrival, 313; control, 449; dichromatism, 126; display, 351; flight, 283, 286; ecology, 210; flock, 239; habits, 232; migration, 305; nesting, 223; polygamy, 349
Blackbird, Yellow-headed (*Xanthocephalus xanthocephalus*): colony, 253; feeding, 384; incubation, 371, 372; mortality, 388; nestling, 386, territory, 226, 229
Blinds, use of, 466–467
Bluebird, Eastern (*Sialia sialis*): abundance, 261; egg, 103; flapping, 277; hovering, 281; migration, 305; nest box, 430; parasites, 405
Bluebird, Mountain (*Sialia currucoides*), 185, 254
Bluebird, Western (*Sialia mexicana*), 185
Bob-white (*Colinus virginianus*), 16, 38, 63, 260, 379; adaptation, 187; age, 137, 138, 142; call, 331; color, 130; covey, 94; distribution, 174, 182; ecology, 210, 230; egg number, 107; erythroism, 126, 395; flight speed, 288; flock, 238, 239; food, 436, 441; heart rate, 87; incubation, 109; laying, 108; mutation, 126; nesting, 371; potato beetle, 444; predation, 251; pseudopolyandry, 349; respiration, 87; sex ratio, 146; size, 186; song, 228, 334; survival, 94; weight, 185, 401; wing load, 276; winter, 300
Bob-white, Masked (*Colinus ridgwayi*), 424
Bobolink: feathers, 118, 123; flight, 283; flight song, 330; migration, 305, 315, 316
Booby (*Sula*), 21
Bowerbird, Satin (*Ptilonorhynchos violaceus*), 353–354
Brain, 20, 54, 63, 73
Breagyps clarki, 156, 157
Breeding, conditions influencing, 360–361
Breeding activities, 356–361
Breeding Bird Census, 469
Breeding potential, 247–249
Breeding seasons, 356–360
Brood patch, 372
Brooding, 382–383
Brush Turkey (Megapodidae), 372, 377
Buarremon, 396
Bunting, 305
Bunting, Indigo (*Passerina cyanea*), 201
Bunting, Lark (*Calamospiza melanocorys*), 176, 281, 283, 330
Bunting, Lazuli (*Passerina amoena*), 283, 330
Bunting, Painted (*Passerina ciris*), 330
Bunting, Snow (*Plectrophenax nivalis*), 164, 283; display, 353, 354; flight, 283; habits, 232; hearing, 336; plumage, 123
Bunting, Townsend (*Spiza townsendi*), extinction, 419, 422
Bursa of Fabricius, 141, 144
Bush-tit (*Psaltriparus minimus*), 167, 283, 349
Bustard (*Otis tarda*), 241
Buteo magnirostris, 209
Buzzard, Common (*Buteo vulgaris*), 436

Cahow (*Pterodroma cahow*), 423
California, 151, 165, 166, 167, 171, 174, 180, 199, 311, 312, 318
Calls, adult and young, 330–331
Cameras, 466
Canary (*Serinus canaria*): brain, 72; cage, 450; disease, 407; egg number, 107; heart rate, 87; heat, 84, 85, respiration, 87
Canvasback (*Aythya valisineria*), 146, 147, 283, 336
Capercailie (*Tetrao urogallus*), 322, 438
Captive birds, 449–450

Caracara, Audubon (*Polyborus cheriway*), 424, 426
Caracara, Guadalupe (*Polyborus lutosus*), extinction, 423
Cardinal (*Richmondena cardinalis*), 44, 153, 164, 166; abundance, 261, 262; age, 135, 136; color, 130; distribution, 176; ecology, 200, 201, 210; feather, 120; flock, 238; needs, 206; nesting, 360, 363, 368; song, 337; temperature, 83; weight, 185, 273; winter, 300, 428
Carduleniae, 153, 166, 195
Care of young, 381–388
Carrying capacity, 211–212, 251, 252
Cassowary (Casuariidae), 36, 40, 71, 162; feathers, 118; incubation, 110; temperature, 83
Catbird (*Dumetella carolinensis*), 243, 368
Cathartidae, 152, 195
Cathartine dynasty, rise and fall, 155–156
Cathartornis gracilis, 156, 157
Cenozoic, 13
Census, 246
Center of gravity, 21–22
Central American water gap, 173, 175
Certhiidae, 195
Chachalaca (*Ortalis vetula*), 28, 284, 342
Chaffinch (*Fringilla coelebs*), 436
Charadriiformes, 163, 166
Chat (*Icteria virens*), 164; distribution, 183; ecology, 200; flight, 283; insecticides, 445; peripheral variation, 160; song, 330, 337
Check lists, 31
Cheel (*Milvus*), 276
Chickadee (Paridae), 54, 153, 195, 368, 461; calls, 153; evolution, 165–166, 167; forest association, 153; habits, 232, 233; migration, 305; needs, 209; nest box, 430; posture, 457; roosting, 207; tail, 284; winter feeding, 428
Chickadee, Alaska (*Parus cinctus*), 166, 167
Chickadee, Black-capped, 247; abundance, 261; calls, 324, 328, 329; feeding, 438; flight, 283; flock, 231, 238; habits, 233; hearing, 281; heart and breathing, 88; migration, 300; minimum area, 252; music, 337, 339, 340, 342, 343; range, 190; weight, 185; wing load, 276
Chickadee, Black-capped and Carolina Chickadee relations, 171–172
Chickadee, Carolina (*Parus carolina*): feather, 120; feeding, 240; music, 339, 340, 342, 343; red cells, 69; temperature, 83
Chickadee, Chestnut-sided (*Parus rufescens*), 165–168, 174
Chickadee, Mountain (*Parus gambeli*), 233, 343
Chicken (*Gallus domesticus*), 15, 16, 18, 45, 46, 50, 53, 61, 70, 75, 118; air sacs, 65; bathing, 410; breeding age, 135; breeds, 161, 398, 399; color, 124, 125; diet, 89; disease, 406, 407; domestication, 451; egg anatomy, 110; egg number, 107; egg passage, 101; egg size, embryo, 108–109, 112; embryo mortality, 373; feather, 120; flock, 231; habits, 232; heart, 87; heat, 84; heredity, 391; incubation, 112; music, 340; mutations, 397; respiration, 66–67; semen volume, 356; sex ratio, 146, 395; weight, 376
Chiffchaff (*Phylloscopus collybita*), 146, 372
Chough (*Pyrrhocorax pyrrhocorax*), 185, 413
Christmas Census, 181, 192, 193, 194, 238, 239, 260, 264, 317
Chuck-will's-widow (*Caprimulgus carolinensis*), 334, 462
Circulatory system, 68–69
Climatic influences, 180–182
Climax, 199, 200
Climograph, 180, 182
Cline, 159, 160
Cloaca, 47, 60, 63, 69, 70
Color, 123–133; abnormal, 125–126; concealing, 129; countershading, 130; display, 129; flash, 130; nature of, 123–125; pattern, 128; recognition, 129; ruptive, 130; semantic, 131; warning, 129; white, 125
Color dilution, 396
Color discrimination, 474
Color of eggs, 102
Color phases, 126, 127, 396
Color uses, 127–133; visual and nonvisual, 127–129
Coloration, concealing, 129–130; display, 131–132; protective, 102; young and nests, 153–154
Columba: heredity, 397; incubation, 110
Commensalism, 240
Commercial use of birds, 452–454
Community relations, 211
Comparison, reptiles, birds, and mammals, 18–20
Competition and segregation, 202
Competition relations, 251–252
Concentration areas, 318
Conclusions, 459

Condor (*Gymnogyps californianus*), 46 155, 156, 157, 165, 424, 425–426; age, 136; distribution, 171; egg number, 107; Pleistocene, 152; respiration, 87
Congregation, 238
Connecticut, 414, 420
Convergence, 163
Cooling, 86–89, 92
Cooper Ornithological Society, 416
Coot (*Fulica americana*), 166; ecology, 200; flock, 239; migration, 305; starvation, 90
Coot (Fulicinae), 357
Copulation, 99, 355–356
Coragyps occidentalis, 156, 157
Cormorant, Double-crested (*Phalacrocorax auritus*), 277, 366–368
Cormorant Pallas (*Phalacrocorax perspicillatus*), 419
Cormorants (Phalacrocoracidae), 44; bounty, 411; flightless, 163; habits, 241; parasites, 404; trained, 450
Corvidae, 42, 58, 59, 195; age, 143; flock, 239; intelligence, 72; nest construction, 110; Pleistocene, 152; speed, 287
Cotingidae, 46, 195
Cotylosaurs, 6, 7
Courser, Black-backed (Crocodile Bird) (*Pluvianus aegyptius*), 372
Courtship, 346; communal, 230; display, 131; flight, 283, 352; function of, 346–347; patterns, 349–350; performances, 350–354
Cover, 170; and community, 205–212; types, 204, 205; volume, 207
Cowbird, Bay-winged (*Agelaioides badius*), 242
Cowbird, Brown-headed (*Molothrus ater*), 165, 209, 347, 459, 470; abundance, 261; albinism, 125; bill, 54; egg, 106; feathers, 118; feeding, 257; flock, 239; heredity, 394; incubation, 106; laying, 108, 235, 369; migration, 300, 305, 308; monogamy, 235, 349; mutation, 240; parasitism, 235, 377; sex ratio, 146; temperature, 83; territory, 223
Cowbird, Red-eyed (*Tangavius*), 165
Cowbird, Screaming (*Molothrus rufoaxillaris*), 242
Cracidae, 28, 195
Crane, Sandhill, 24, 63, 72, 322
Crane, Whooping (*Grus americana*), 63, 424, 427; anatomy, 322; migration, 158; numbers, 241, 261; range, 190; voice, 322
Cranes (Gruidae), 152, 166, 195; eggs, 249; flocks, 237; habits, 233; migration, 304, 305
Cranial nerves, 73, 74
Creeper, Brown (*Certhia familiaris*), 41, 286, 336, 443
Crests, 44–46
Cretaceous birds, 12–13, 37
Crocodile, 7, 17, 23, 142
Crop, 60, 61
Crossbill (*Loxia*), 42, 61, 166; color, 125, distribution, 175; flight, 283; flight years, 303; migration, 303; plumage, 122; salt licks, 92, 443
Crow (*Corvus brachyrhynchos*), 18, 58, 59, 126, 242, 433, 461, 474; abundance, 261; adaptation, 187; age, 143, 144; albinism, 125; brain weight, 72; ecology, 210; eggs, 249; feeding, 384; flapping, 277; flock, 238, 239; growth, 377; hearing, 335; migration, 304; nest, 364; roosting, 225; sex ratio, 146; temperature, 83; visual distance, 465; weight, 185; wing load, 276
Cruising distance, 206
Cuckoo, European (*Cuculus canorus*): cartoon art, 414; egg-host size, 105; ejection of nest mates, 235; hatching, 376; laying, 369; migration, 305; parasitism, 234–235
Cuckoos (Cuculidae), 183, 195; gizzard lining, 62; Pleistocene, 152; syrinx, 321; toes, 48
Cuckoos, American (*Coccyzus*): ecology, 206; incubation, 109; song, 338; tail, 284
Curassow, Crested (*Crax rubra*), 28, 45; bill, 44, 45; crest, 45; roosting, 209
Curlew, 166, 283
Curlew, Bristle-thighed (*Phaeopus tahitiensis*), 190
Curlew, Eskimo (*Numenius arquatus*), extinction, 419
Cycles: flight years, 303–304; population, 258–259

Daily rhythm, 82, 213
Daily temperature changes, 82
Day length, 91–92, 213, 295, 474
Densities, mixed, 254–256
Density and changes, 253–260
Destruction of nests, 372–373
Diatryma, 162
Dickcissel (*Spiza americana*), 164; ecology, 201; invasions, 171, 172; music, 340
Diets, 89
Dinosaur, 6–9

Dipper (*Cinclus*), 78, 166, 195, 283
Disease, 406–408
Display, 131–132, 323, 350–354; diversionary, 387
Display flight, 283, 352
Display season, 227, 233
Distinguishing characteristics of birds, 15–16
Distinguishing features of birds, 22–23
Diving, 277
Dodo (*Raphus cucullatus*), 163, 423
Domestication, 449–452
Dominance, genetic, 390–392
Dominance, social, 230–233; age, 231–232; interspecies, 232–233; sex, 232
Dove, Mourning (*Zenaidura macroura*): abundance, 255, 261; age, 137, 138, 142; eggs, 249; feathers, 118; flapping, 277; flight, 283; food, 256, 436; freezing, 409; laying, 369; migration, 305, 307; mortality, 139; nesting, 360, 368; salt, 443; sex ratio, 146; song, 332; temperature, 83; territory, 220; weight, 185; wind, 218
Dove, Rock (*Columba liva*), 63; brain, 73; breeds, 161; domestication, 452; flapping, 277; hearing, 336; mutations, 397; nesting, 223; sex ratio, 495
Dove, Spotted (*Spilopelia chinensis*), 260
Dove, Stock (*Columba aenas*), 106
Dove, White-winged (*Zenaida asiatica*), 424; drinking, 92; drought, 217; killing, 421; migration, 292; nesting, 237; salt, 443
Dovekie (*Plautus alle*), 438
Doves (Columbidae): age, 144, 195; drinking, 92; egg number, 370; food, 436; heat, 84, 85; hybrids, 399; nesting, 237; Pleistocene, 152; salt licks, 92
Drinking habits, 443
Drongo (*Dicrurus paradiseus*), 160
Drought, 217
Drumming, 324; drumming flight, 324
Duck, Black (*Anas rubripes*), 144, 237
Duck, Labrador (*Camptorhynchus labradorius*), 190, 419–420
Duck, Mallard (*Anas platyrhynchos*), 39, 122, 350; age, 135, 144; egg number, 107; feathers, 118; feeding, 441, 442; flight speed, 288; habits, 232; hybrids, 398; sex ratio, 146; sex recognition, 347; temperature, 83; voice, 330; wing load, 267
Duck, Mallard-Black, distribution, 192, 193
Duck, Mottled (*Anas fulvigula*), 283
Duck, Pintail (*Anas acuta*), 64, 146, 348, 398
Duck, Redhead (*Aythya americana*), 288
Duck, Ruddy Shell (*Cascara ferrugina*), 96, 232
Duck, Scaup (*Aythya marila*), 457
Duck, Shoveller (*Spatula clypeata*), 63, 144
Duck, Tree (*Dendrocygna*), 63, 283
Duck, Wood (*Aix sponsa*), 63, 122, 189
Ducks, 21, 47, 61, 71, 78, 119, 249, 368, 379; domestication, 451, 452; ecology, 200, 210; flight, 284; flocks, 237; heart rate, 87; hybrids, 398; migration, 301, 305; navigation, 307; ovary, 197; parasites, 405, respiration, 87; sex ratio, 146; sickness, 406–407; temperature, 82; voice, 330
Dunlin (*Erolia alpina*), 330, 436
d-v-p system, 67

Eagle (protection), 411; totem art, 413; visual acuity, 76
Eagle, Bald (*Haliaeetus leucocephalus*): age, 141, 144; breeding season, 359; habits, 242; mating, 257; nest, 363, 373; plumage, 122; protection, 424; vagrant migration, 302, 474
Eagle, Golden (*Aquila chrysaetos*): feathers, 120; habits, 441, 442; range, 190; territory, 229; weight, 273; wing load, 267
Eagle, Harpy (*Harpyhaliaetus*), 439
Ear, 78–79
Ecological factors of distribution, 169
Ecological field studies, 438, 472–473
Ecological homologues, 35, 163
Ecological occupation and success, 149
Ecological segregation, 187, 201
Ecological succession, 199–200
Economic values, 431–454
Ecotone, 179, 207
Egg, 99–108; abnormal, 102; anatomy, 110; determinant number, 107; incubation, 369–373; indeterminant number, 107; initial growth, 99–100; laying time, 108; markings, 102; number, 107; passage, 99, 101; percentage of shell, 99; pigment, 102; shape, 100–101; size, 103, 104, 106; specific gravity, 105; success, 248–249, 253, 373; turning of, 110; volume, 105; weight, 104–107
Egg color, 102–103
Egging, 453
Egret, 431; age, 142; migration, 305; mutualism, 240; plumage, 118, 417; roosting, 213; weight, 64
Eider, 39, 453

Elephant Bird (*Aepyornis maximus*), 36, 104, 110
Emberizinae, 153, 166, 195
Embryo, 108–112
Embryonic development rate, 109–110, 112
Emu (Dromiceidae), 36, 40, 71, 162; egg color, 102; egg weight and incubation, 106; feathers, 118
Emu-wren (*Stipiturus*), 42, 299
Endemic and native, 168
Endocrine system, 71–72
Energy: base, 81, 198–199; competition, 81; intake, 84; needs and air temperature, 86; resources, 93–94; use of, in flight, 272
Environment and flight, 284–286
Environmental adaptations, 35–37
Eocene, 173
Equilibrium, 79, 80
Equipment, field, 460–468
Eruthroism, 126
Evolution, behavior, 152–153
Evolution and adaptation, 149–150
Evolution and adaptive radiation, 163–165
Evolution and ecological factors, 154–157
Evolution and spread, 163–168
Evolution in recent past, 151–152
Evolution of coloration, 153
Evolution of habits, 148–154
Evolution of nesting, 369
Evolution of structure, 148–154
Evolutionary characters, 148–150
Evolutionary succession, 155–156
Excretory system, 69–70
Exotics in new environment, 259–260
Extinct species, 418–423
Extinction threshold, 253
Eye, 42, 54; shine, 52; size, 75; weight, 64

Fahrenholz Rule, 405
Faisáno Real (Curassow), 45, 46
Falcon (Falconidae), 21, 29, 30; eyries, 158; flight, 284; flight speed, 287; flock, 239; heart, 87; Pleistocene, 152; predation, 170
Falcon, American Sparrow (*Falco sparverius*), 29–30; color, 125; flapping, 277; flight, 283; food, 436, 442; habits, 189; hovering nest, 430; territory, 223; weight, 64, 185; wing load, 276
Falcon, Aplomado (*Falco femoralis*), 424
Falcon, Peregrine (*Falco peregrinus*): ecology, 170; nesting, 158; range, 174; speed, 288; wing load, 267
Falcon, Prairie (*Falco mexicanus*), 164; ecology, 170; flight, 283; migration, 300; mutualism, 241; vision, 76
Falconiformes, 28, 97, 110, 151, 152
Falconry, 450
Fall recrudescence, 99, 331
Family, 28, 33
Fat deposition, 91, 294, 295
Feathers, 116–117, 120, 143; kinds, 114–116; number, 118; origin, 113; powder down, 114–116; sound producing, 325–327; structure, 117–118; tracts, 113–114, 115
Feeding: incubation and courtship, 354–356; summer, 429; winter, 427–430
Feeding of young, 376, 377, 384–385
Ferae Naturae, 415
Fertilization, 99
Field records and notes, 460–461; techniques, 468–472
Finch, Darwin (Geospizinae), 361
Finch, House (*Carpodacus mexicanus*): adaptation, 187; distribution, 176; exotic, 260; flight song, 330; nest, 430; salt, 443
Finch, Purple (*Carpodacus purpureus*), 92, 142, 305, 340, 443
Finch, Rosy (*Leucosticte*), 166, 174; migration, 301; nest, 359; mouth sac, 384, 385; roosting, 208
Finches (Fringillidae), 61, 209, 470; bill, 44; calls, 331; ecological segregation, 201; egg number, 376; egg size, 104; hybrids, 391; music, 340, 344; origin, 195; plasticity, 153; radiation, 166; winter feeding, 428
Firecrest (*Regulus ignicapillus*), 176
Fish, flying, 269, 270
Flamingo (*Phoenicopterus*), 233
Flicker (*Colaptes*), 19; display, 131, 132; distribution, 192; egg, 106; hybrids, 391; nest, 430
Flicker, Red-shafted (*Colaptes cafer*), 192; distribution, 175; feathers, 121; speed, 288; totem art, 413; xanthochroism, 126
Flicker, Yellow-shafted (*Colaptes auratus*), 126, 192; distribution, 175; eggs, 107; flapping, 227; mustache, 131, 347
Flight: adaptations, 20–22; bird, 266–288; feeding, 282–283; gliding, 280–281; kinds of, 278–282; limits, 171; maneuvering, 277; modifications, 39; muscles, 22, 51, 52; nuptial, 352; power, 278–280; singing, 281, 324, 326; sinking speed, 280; soaring, 280–281; song, 325–326, 329–330; special, 281–282;

speed, 287–288; structures, 272–273; tail length, 40
Flight and environment, 284–286
Flight in vertebrates, 269–272
Flight years, 303–304
Flightless, 161–163
Flocking, 237–240; advantages, 239–240
Flocks, 238; persistence, 396; size, 238, 239
Flycatcher (*Petroica multicolor*), 158
Flycatcher (Tyrannidae), 166, 193, 195, 368; flight, 282; hovering, 282; migration, 292, 305
Flycatcher, Acadian (*Empidonax virescens*), 200
Flycatcher, Ash-throated (*Myiarchus cinerascens*), 100
Flycatcher, Crested (*Myiarchus crinitus*), 189, 254, 430
Flycatcher, Least (*Empidonax minimus*), 189
Flycatcher, Pied (*Muscicapa hypoleuca*), 234
Flycatcher, Royal (*Onychorhynchus*), 45
Flycatcher, Scissor-tailed (*Muscivora forficata*), 41; food, 384; growth, 379; flight song, 283, 330, 340; tail, 149
Flycatcher, Vermilion (*Pyrocephalus rubinus*), 283, 329, 330, 352
"Flyways," Waterfowl, 311
Florida, 151, 152, 171, 190, 211, 421, 422
Fluctuations, cyclic, 258–259
Food, coniferous forage, 437; consumption, 90, 91, 436–437; habits, 434–442; special, 442–443; storage, 443
Food adaptations, 435
Food chain, 251, 443–444
Foot adaptations, 46–48
Fossils, 6, 11, 12, 13, 25, 148, 151
Fossorial world, 36
Frequency (song), 335–337
Frigate; *see* Man-o'-war Bird
Frog, Flying, 269, 271
Fulmar (*Fulmarus glacialis*), 253, 406

Gadwall (*Anas strepera*), 39
Galliformes, 28, 29, 69, 148
Gallinule, 47, 200, 370
Gannet (*Moris bassana*), 63; colony, 253; courtship, 355; egg number, 370; habits, 241
Generalizations, 459
Genus, 26–28
Geographic complements, 191–192
Geographic variation of egg success, 249–250
Geologic Time Scale, 10
Germ layers, 110–112
Gizzard, 22, 60, 61–62
Gloger Rule, 167, 185, 186
Gnatcatcher, 195
Gnorimopsar, 164
Godwit (*Limosa*), 283
Going afield, 462–463
Golden-eye (*Bucephala*), 39
Goldfinch, American (*Spinus tristis*), 166, 431; abundance, 261; bathing, 410; distribution, 176; ecology, 201; eggs, 370; feeding, 375, 384; flapping, 277; flight, 286; hatching, 376; migration, 305; nest, 359, 362, 364; song, 332; visual distance, 465
Goldfinch, British (*Carduelis carduelis*), 260, 436
Gonads, 96–98, 99
Goose, 16, 119; distribution, 451; eggs, 249; flight, 287; flocks, 223, 237; food, 436, 437, 438, 441; heat, 84, 85; hybrids, 398; laying, 108; migration, 298, 301, 305, 313; pairing, 348; parasites, 405; respiration, 87; sounds, 324
Goose, Blue (*Chen caerulescens*), 126, 221
Goose, Canada (*Branta canadensis*), 63, 379; flight, 284, 288; flock, 239; migration, 299, 304, 315; nest, 368; temperature, 83; territory, 221; weight, 273
Goose, Falkland (*Chloephaga*), 149
Goose, Nene (*Nesochen sandvicensis*), 149
Goose, Ross (*Chen rossi*), 190, 261, 311, 423, 425
Goose, Snow (*Chen hyperborea*): color, 125, 126; migration, 317; numbers, 246, 261; territory, 221
Goose, White-fronted (*Anser albifrons*), 63
Goshawk (*Accipiter gentilis*), 146, 164, 239, 303, 415
Grackle (*Quiscalus*), 124, 165, 261, 283, 429, 470; albinism, 125; "buccal lathe," 441; egg, 100; respiration, 87; roosting, 213; weight, 64, 185
Grackle, Boat-tailed (*Cassidix mexicanus*), 146, 149, 223, 330
Grassquit (*Volatinia jacarinia*), 330
Grebe, 16, 48, 152, 354; ecology, 200; egg, 101; flightless, 163; temperature, 83
Grebe, Black-necked (*Podiceps caspicus*), 264
Grebe, Pied-billed (*Podilymbus podiceps*), 264
Grebe, Western (*Aechmophorus occidentalis*), 83, 417
Greenshank (*Tringa nebularia*), 330

Gregariousness, 237, 239
Grosbeak, 301, 305
Grosbeak, Black-headed (*Hedymeles melanocephalus*), 335, 371, 372
Grosbeak, Evening (*Hesperiphona vespertina*), 44, 92, 153, 303, 359
Grosbeak, Pine (*Pinicola enucleator*), 92, 185, 186, 303, 384
Grosbeak, Rose-breasted (*Hedymeles ludovicianus*), 136, 142, 164, 166, 201
Group adherence, 237, 253
Grouse (Tetraonidae), 28, 29, 35, 42, 157, 195, 334, 379; broods, 384; display, 132; eggs, 107, 249; gliding, 280; hybrids, 391; life expectancy, 135; migration, 305; polygamy, 349; promiscuity, 349; tail, 284; vertical flight, 281; voice, 322
Grouse, Black (*Lyrurus*), 42, 323, 349, 438
Grouse, Blue (*Dendragapus obscurus*), 41, 157; broods, 282; color, 29, 130; disease, 406; display, 132; distribution, 172–173, 175; drumming flight, 324; food, 438; habits, 224; migration, 156, 297, 298, 301; radiation, 164
Grouse, Franklin (*Canachites canadensis franklini*), 129, 175, 261, 323, 424
Grouse, Ruffed (*Bonasa umbellus*), 28–29, 35, 157, 172; color, 126, 129, 396, counts, 247; cycles, 259; distribution, 187; drumming, 324, 325, 333, 334; eggs, 107; feeding, 254, 256, 438; injuries, 409; minimum area, 252; nest, 365; parasites, 404; radiation, 164; recrudescence, 331; roosting, 208; tularemia, 407; young, 111
Grouse, Sage (*Centrocercus urophasianus*), 157, 423; courtship, 349; display, 322, 324; ecology, 230; food, 437; habits, 232; territory, 221; viability of sperm, 356
Grouse, Sand (Pterochlididae), 217, 301, 303
Grouse, Scotch (*Lagopus scoticus*), 119, 158
Grouse, Sharp-tailed (*Pedioecetes phasianellus*), 157, 164; courtship, 349; display, 323; distribution, 187; migration, 297; roosting, 209; voice, 322, 323, 324
Grouse, Siberian Spruce (*Canachites falcipennis*), 172, 438
Grouse, Spruce (*Canachites canadensis*), 157, 423; adaptation, 188; color, 129; distribution, 172, 175, 187; food, 438; voice, 323
Growth rate of young, 377–399
Guan (Penelopinae), 28
Guano, 218, 452–453
Guinea Fowl (*Numida meleagris*), 452
Gull, California (*Larus californicus*), 145, 442
Gull, Glaucous (*Larus hyperboreus*), 89, 118
Gull, Great Black-backed (*Larus marinus*), 135, 176, 229, 277, 348
Gull, Herring (*Larus argentatus*), 63, 224; age, 135, 137, 138, 141, 145; colonies, 253; feeding, 355; flapping, 277; life expectancy, 135, 139, 140; migration, 298; mortality, 139; sex ratio, 146
Gull, Laughing (*Larus atricilla*), 277
Gull, Lesser Black-backed (*Larus fuscus*), 253
Gull, Ring-billed (*Larus delawarensis*), 64
Gulls (Laridae), 431; banding, 471; disease, 407; drinking, 92; feeding, 282; flocks, 239; habits, 241; hatching, 376; migration, 305; navigation, 307; plumage, 122; parasites, 402, 404; roosting, 209; soaring, 281
Gymnogyps amplus, 156, 157

Habitat choice, 200–203, 210
Harrier, Marsh (*Circus cyaneus*), 164, 349; courtship, 352; distribution, 182; flight, 283, 330; hovering, 281; nestlings, 386; wing load, 276
Hatching and young, 375–377
Hawaii, 149, 155, 418
Hawk, 19, 38, 61, 74, 280, 368, 433; decline, 414, 415; disease, 407; eggs, 249, 370; eye, 76; hatching, 376; hybrids, 398; melanism, 126; migration, 298, 305; nestling, 386; powder down, 116; rodent control, 447; soaring, 282; visual acuity, wind, 218
Hawk, Broad-winged (*Buteo platypterus*), 164, 465
Hawk, Cooper (*Accipiter cooperi*), 130, 192, 239, 415, 443
Hawk, Ferruginous Rough-legged (*Buteo regalis*), 164
Hawk, Gray (*Buteo nitida*), 424
Hawk, Harris (*Parabuteo unicinctus*), 424
Hawk, Mexican Black (*Buteo gallus anthracinus*), 424
Hawk, Red-bellied (*Buteo lineatus elegans*), 424
Hawk, Red-shouldered (*Buteo lineatus*), 87

Hawk, Red-tailed (*Buteo jamaicensis*), 177, 242
Hawk, Rough-legged (*Buteo lagopus*), 126, 164, 281, 283
Hawk, Sennett White-tailed (*Buteo albicaudatus*), 424
Hawk, Sharp-shinned (*Accipiter striatus*), 120, 164, 192, 239, 443
Hawk, Short-tailed (*Buteo brachyurus*), 424
Hawk, Swainson (*Buteo swainsoni*), 26
Hawk, Zone-tailed (*Buteo albonotatus*), 424
Hawk Mountain, 218
Hearing, 78–80, 335–336
Heart, 68, 75; rate, 86; size, 18, 19, 68; weight, 64
Heat control, 82–89
Heath Hen (*Tympanuchus cupido cupido*), 253, 419, 420–421
Hemoglobin, 69, 82, 124
Heredity, 112, 125, 126, 390–399
Heron (Ardeidae), 21, 78; banding, 469; eggs, 370; hatching, 376; migration, 298, 305; nest, 368; parasites, 405; Pleistocene, 152; powder down, 116; protection, 411; temperature, 82
Heron, Black-crowned Night (*Nycticorax nycticorax*), 214, 288, 469
Heron, Great Blue (*Ardea herodias*), 223, 246, 288, 441
Heron, Great White (*Ardea occidentalis*), 423, 424
Heron, Green (*Butorides virescens*), 38, 213
Heron, Little Blue (*Florida caerulea*), 213
Hesperornis, 155, 162, 212
Hibernation, 306
High-jacking, 241–242
Hoatzin (Opisthocomidae), 38, 61
Honey-creeper (Coerebidae), 195
Honey-creeper, Hawaiian (Drepanididae), 155
Honey-eaters (Meliphagidae), 147
Honey Guide, Lyre-tailed (*Melichneutes robustus*), 42, 330
Honey Guides (Indicatoridae), 234, 236
Hoopoe (*Upupa epops*), 193
Hornbill (Bucerotidae), 44, 62, 354, 369, 371
Humidity influences, 92–93, 216–217
Hummingbird (Tochilidae), 38, 39, 61, 124, 193, 195; display, 132; eggs, 104; flight, 281, 282, 283; hovering, 281; hybrids, 398; incubation, 110; migration, 292; parasites, 405; plumage, 417; pollination, 446–447; temperature, 83; visual distance, 465
Hummingbird, Allen (*Selasphorus alleni*), 312, 371
Hummingbird, Broad-tailed (*Selasphorus platycercus*), 106
Hummingbird, Ruby-throated (*Archilochus colubris*), 101, 106, 118, 275, 276, 279, 307, 384, 438
Hummingbird, Violet-eared (*Colibri thassinus*), 352
Hybrids, 391, 398
Hyoid, 55, 60

Ibis (Threskiornithidae), 152, 423
Ibis, Wood (*Mycteria americana*), 79
Ichthyornis, 13
Ichthyosauria, 19
Icteridae, 42, 47, 53, 193, 195; flocks, 239; nest, 362; radiation, 166; social parasitism, 234
Idaho, 166, 298
Ill-situated birds, 400
Illinois, 206, 422
Impressionable age, 379–381
Imprinting, 209, 347, 379
Incubation, 106, 109–110, 371–372
Indiana, 422
Influence: altitudinal, 215–216; instinctive needs, 209
Influence of mobility, 190
Injuries, 409
Injury feigning, 132, 387
Insect suppression, 444–445
Insecticides, 444–445
Instinctive calls and songs, 324–326
Intelligence, 72
Intercompensation, 251
International Rules of Nomenclature, 29, 30, 31
Interspersion, 191, 205–206
Intolerance of change, 186–189
Intoxication, 408
Intraspecies distribution, 185–186
Inversity, 247
Island birds, 155, 271; evolutionary traps, 155; flightlessness, 161–163; island hoppers, 173, 175
Isolation, 26, 151, 155, 156, 346–347

Jabiru (*Ephuppiorhynchus*), 152
Jacana, 47
Jacamar (Galbulidae), 386
Jackdaw (*Corvus monedula*), 221, 227
Jaeger (*Stercorarius*), 241
Jay, Blue (*Cyanocitta cristata*), 87, 121; abundance, 87, 211; adaptation, 188;

Jay, Blue—*continued*
color, 124, 396; competition, 252; distribution, 176; ecology, 200, 210; egg, 100; food, 443; spread, 189; weight, 185; wing flapping, 277, 278; winter feeding, 428
Jay, Canada (*Perisoreus canadensis*), 26–27, 89, 166, 359
Jay, Cissa (*Cissa*), 123
Jay, Gray (*Perisoreus canadensis griseus*), 182
Jay, Oregon (*Perisoreus canadensis obscurus*), 174
Jay, Scrub (*Aphelocoma coerulescens*), 114, 115
Junco, 164, 166, 301, 392, 428
Junco, Slate-colored (*Junco hyemalis*), 94; abundance, 255, 261; distribution, 175; flocks, 238, 328; food, 442; instincts, 435; recognition, 131
Jungle Fowl, 63; breeding age, 135; domestication, 451; egg number, 107; incubation rate, 112
Jurassic, 6, 10–12

Kansas, 13, 421, 422
Kentucky, 421, 422
Kidney, 64, 70
Killdeer (*Charadrius vociferus*), 462; color, 128; egg, 100, 103; flapping, 277; injury feigning, 132; numbers, 255
Kingbird, 272, 305
Kingbird, Eastern (*Tyrannus tyrannus*), 185, 384
Kingbird, Gray (*Tyrannus dominicensis*), 292
Kingbird, Western (*Tyrannus verticalis*), 176, 185
Kingfisher (Alcedinidae), 28, 36, 174, 183, 195, 376, 439, 443
Kingfisher, Belted (*Megaceryle alcyon*), 223, 277, 281, 364, 386
Kinglet (Regulidae), 305
Kinglet, Golden-crowned (*Regulus satrapa*), 261, 281, 336
Kinglet, Ruby-crowned (*Regulus calendula*), 132, 273, 353
Kite (*Milvus*), 411, 415
Kite, Everglade (*Rostrhamus sociabilis*), 174, 424, 426, 439
Kite, Mississippi (*Ictinia misisippiensis*), 424, 426
Kite, Swallow-tailed (*Elanoides forficatus*), 424, 426
Kite, White-tailed (*Elanus leucurus*), 424, 426
Kiwi (*Apteryx*), 63, 71, 162, 163; egg, 104, 105; temperature, 83
Knot (*Calidris canutus*), 28

Lambert's law, 85
Lammergyer (*Gypaëtus barbatus*), 216
Lapwing (*Vanellus vanellus*), 138, 139, 176, 301, 436
Lark (Alaudidae), 195, 218, 281
Lark, Horned (Otocoris alpestris), 166; abundance, 261; distribution, 179; early song, 331; ecology, 200; flight, 283; flight song, 330; hearing, 336; hovering, 281; incubation, 109; nesting, 359; range, 190; spread, 189; temperature, 83; weight, 185
Larynx, 320
Latitude and altitude similarity, 216
Laying hours, 369
Leaving the nest, 386–387
"Left-handedness," 393
Lethal characters, 395
Lichmera, 147
Life equations, 250
Life expectancy, 135–136
Life form, 179
Life hazards, 248, 249
Life zones, 177–179, 204
Lift, 272, 273
Light influence, 213–214, 360
Limiting factors, 250–251
Limits of tolerance, 35
Linnaeus, 30, 31, 32
Linnet (*Carduelis cannabina*), 176
Liver, 63, 64
Lizards (Squamata), 7, 271
Longevity, 135–136, 253
Longspur (*Calcarius*), 46, 283, 305
Loon (*Gavia immer*), 48, 354; eggs, 102, 370; migration, 305; weight, 64
Loss: nests and eggs, 372–373; of young, 149; population, 137
Louisiana, 147, 307, 422
Lungs, 61, 64, 65, 66–68
Lure of nature, 4, 455–456
Lymph, 69
Lyre Bird (*Menura novaehollandiae*), 42

Macaw, Cuban Tri-colored (*Ara tricolor*), 423
Macaw, Gosse (*Ara gossei*), 423
Macaw, Guadeloupe (*Ara guadeloupensis*), 423
Macroclimate, 202
Magpie (*Pica*), 411; flight, 283; flight

speed, 288; nest, 363; range, 190; spread, 195
Maine, 419
Major habitats, 203
Mammals, flying, 271–272
Mamo (*Drepanis pacifica*), 453
Man-o'-war Bird (*Fregata magnificens*), 241, 273, 450
Manakin (Pipridae), 195, 326, 327
Manitoba, 147, 421
Maps, 460
Marginal habitat, 209
Marking birds for identificaton, 471–472
Martin, Purple (*Progne subis*), 189; arrival, 313; flapping, 277; flight, 286, 287; nest box, 430; wing load, 276
Martin, Sand (*Riparia riparia*), 183; *see also* Swallow, Bank
Massachusetts, 263, 298, 308, 414, 419, 420
Mating habits, 348–349
Maturity, deferred, 349
Meadowlark (*Sturnella*), 166; abundance, 255, 261; calls, 331; color, 128, 130; distribution, 174, 182; ecology, 200, 210; flight song, 330; music, 344; roosting, 208; territory, 226
Meadowlark, Eastern (*Sturnella magna*), 328; music, 337, 339, 340, 342, 343
Meadowlark, Western (*Sturnella neglecta*), 83; music, 337, 339, 340
Measurements afield, 457–458
Medical nostrums, 453–454
Melanism, 60, 126, 396
Merganser (*Mergus*), 42, 144, 313, 318
Merganser, Hooded (*Lophodytes cucullatus*), 45
Mesozoic, 6, 8–13, 19, 269
Mesozoic birds, 10–12
Metabolic rate, 72, 83–86
Michigan, 199, 201, 246, 313, 342, 360, 421, 422
Microclimates, 183, 202
Migration, 94, 289; advantages, 306; altitude, 304; concepts, 289–294; controls, 294–297; cues, 309; disadvantages, 306–307; diurnal, 305–306; early accounts, 289–290; early ideas, 290–291; fall, 315; flocks, 239–240; general pattern, 309–318; habits, 297–309; influences, 295–297; internal influences, 292–293; kinds, 300–303; molt-migration, 301; navigation, 307–309; nocturnal, 305–306; origin, 291–294; pathways, 309–311; premigration events, 311–312; sequence, 313, 315; sporadic, 301; spring, 313–315; study of, 474; theories, 308–309; use of telescopes, 305–306; winter range, 315–318
Migratory bird treaties, 415–416
Minerals, 92, 107, 442
Minimum area and numbers, 252–253
Miocene, 25, 151, 152, 162, 173
Mississippi, 421, 422
Missouri, 422
Mitotic rate, 93, 436
Moa (Dinornithidae), 35, 36, 62, 162, 411
Mobility and range, 190
Mockingbird (*Mimus polyglottos*), 167; abundance, 261; age, 138; color, 130; distribution, 176; evening song, 213; flight song, 283, 330; gliding, 280; habits, 224; movement, 307; music, 342; needs, 206; nest, 368; night song, 333; range, 190; tail, 284; variations in mocking, 160; water, 429; wing flashing, 243; winter feeding, 428
Moisture, 216–217
Mollymauk, Buller (*Diomedea bulleri*), 372
Molt, 116, 119–123, 142
Moltless change, 122–123
Monogamy, 348
Monuments: Gull, 442; Passenger Pigeon, 421
Montana, 166
Morphology and taxonomy, 25
Mortality, differential, 349
Mortality of young, 135, 150, 388
Mortality rate, 139
Motmot (Momotidae), 41, 386
Mound Bird; *see* Brush Turkey
Mouth, 60
Murre, California (*Uria aalge*), 107
Muscle system, 57–59; efficiency, 81; kinds, 57; operation, 51, 52, 57; weight, 279
Music, 319–345; amphibians, 339; bird song, 337–344; essentials, 338–339; similarities of bird and human, 319; scales, 341–342; scores, 329, 338, 340, 344
Mutations, 149, 395–397
Mutualism, 240–241
Mynahs (Sturnidae), 450, 460
Myzomela, 147

National Audubon Society, 416
Navigation, 307–309
Nebraska, 422
Needs of a species, 169–171
Neognathae, 29
Neornithes, 29, 33
Nervous system, 72–73

Nest and egg losses, 372–373
Nest and nesting, 361–369; construction, 110, 369; destruction, 370–371; early, 109; hole-nesters, 102–103; location, 365–368; material, 362–364; multiple; 370–371; protection, 382–384; sanitation, 385–386
Nest site selection, 361–362, 429–430
Nesting: origin and evolution, 368–369; season variations, 360
Nestling period, 386
New Jersey, 213, 308, 414, 420, 422
New York, 313, 363, 421
New Zealand, 36, 62, 155, 162, 260, 423
Niche, 155, 202
Nictitating membrane, 76
Nighthawk (*Chordeiles*), 213, 462; cooling by gular fluttering, 188; display flight, 352; egg, 103; feeding, 282; flight, 283; hatching, 376; migration, 305; roosting, 208; syrinx, 17, 83; torpid, 306; vision, 78; wing load, 276
Nighthawk, Pennant (*Cosmetornis vexillarius*), 39
Nomenclature, 24
Nonadaptive characters, 34
North Carolina, 254, 421
Notochord possession, 14
Notornis, 162, 423
Nova Scotia, 420, 421
Number: birds, 260–265; changes with time, 261–263; genera, 32; Pleistocene species, 151; present species, 32
Nutcracker (*Nucifraga*), 195
Nutcracker, Clark (*Nucifraga columbiana*), 175, 301
Nuthatch (*Sitta*), 61, 195, 368, 461; food, 443; habits, 232; needs, 209, nest box, 430; posture, 457; winter feeding, 428
Nuthatch, European (*Sitta europaea*), 372
Nuthatch, Red-breasted (*Sitta canadensis*), 191; courtship, 353; flight, 283; habits, 233; migration, 303
Nuthatch, White-breasted (*Sitta carolinensis*), 83, 233, 238, 261
Nutrition, 89–90

Observational techniques, 456–459
Odontophorinae, 195
Ohio, 213, 262, 318, 420
Oil Bird (*Steatornis caripensis*), 453
Oil droplets, 78, 213
Oil gland, 116
Oklahoma, 422
Oligocene, 157, 173
Order, 28–29, 33
Oregon, 199
Orientation to wind, 80
Origin of adaptations, 34–35
Origin of birds, 6–13
Origin of flight, 266–268
Origin of North American bird life, 192–199
Origin of Social Parasitism, 235–237
Oriole (*Icterus*), 305, 364
Oriole, Alta Mira (*Icterus gularis*), 363, 364
Oriole, Baltimore (*Icterus galbula*), 87, 100, 176, 364
Oriole, Golden (*Oriolus oriolus*), 176
Oriole, Orchard (*Icterus spurius*), 100, 166
Oriole, Scott (*Icterus parisorum*), 166
Ornithischia, 6, 7
Ornithomimus, 9
Ornithophillus plants, 446–447
Ornithosuchus, 7
Oropendola (*Zarhynchus wagleri*), 292
Orthogenesis, 149
Osprey (*Pandion haliaetus*), 48; food, 441; habits, 189, 242; numbers, 262; range, 190; red cells, 69; wing load, 267
Ostracoderm, 8
Ostrich, 18, 19, 36, 38, 47, 48, 63, 71, 162, 379; brain, 42; egg, 101, 102, 104, 106; eye, 75; farming, 450; incubation, 106, 110; migration, 297; plume, 118; sounds, 324; weight, 64
Ovaries, 71, 96, 97–98
Ovenbird (*Seiurus aurocapillus*), 164, 459; age, 135, 369; ecology, 202; feeding, 384; flight, 283; flight song, 330, 353; hatching, 376; incubation, 372; life expectancy, 235; mortality, 388; territory, 229
Ovulation, 108
Owl, 16, 61, 195, 213, 368, 433; decline, 414, 415; disease, 407; ear, 80; egg, 249; eye, 76; female voice, 330; flock, 239; incubation, 110; Pleistocene, 152; prey detection, 78; prey selection, 153; roosting, 208; syrinx, 321; temperature rhythm, 82; vision, 77–78
Owl, Barn (*Tyto alba*), 195; brewery, 447; nest box, 430; range, 190; respiration, 87; vision, 78
Owl, Barred (*Strix varia*), 164; flight power, 275; flocking, 239; respiration, 87; vision, 78; weight, 273; wings, 275, 276
Owl, Burrowing (*Speotyto cunicularia*), 36, 63, 164, 174, 241; Florida, 424
Owl, Eagle (*Bubo bubo*), 136
Owl, Elf (*Micropallas whitneyi*), 164

Owl, Horned (*Bubo virginianus*), 45, 48, 63, 335; breeding season, 358; decline, 415; early nesting, 359; egg, 100; female voice, 330; fishing, 441; hearing, 336; incubation, 109; nesting, 242; predation, 251; range, 100; rat and cat control, 447; respiration, 87; sclerotic ring, 76; temperature, 83
Owl, Little (*Athene noctua*), 436
Owl, Long-eared (*Asio asio*), 78, 164
Owl, Pygmy (*Glaucidium gnoma*), 126, 334, 396
Owl, Screech (*Otus asio*), 384; color phase, 126, 396; flocking, 239; habits, 189; hearing, 335; nest box, 430, song, 333; weight, 185, 273
Owl, Short-eared (*Asio flammeus*), 164, 283, 435, 447
Owl, Snowy (*Nyctea nyctea*), 164, 259, 283–284, 303
Owl, Tawny (*Strix aluco*), 436
Ownership of birds, 415
Ox-pecker (*Buphagus*), 240
Oxidation, 82
Oyster-catcher (*Haematopus palliatus*), 283

Palaeoborus rosatus, 25
Palaeogyps prodromus, 157
Pancreas, 63
Parakeet, Shell (*Melopsittacus undulatus*), 232
Paranyroca magna, 25
Paraquet: Carolina, 419, 422; Louisiana, 419, 422
Parasite-host adjustment, 405–406
Parasites: external, 405–406; internal, 401–405; nest, 405
Parrot (Psittacidae), 38, 54, 61, 78, 193, 368; age, 136; caged, 450; disease, 406; distribution, 183; heat, 84; incubation, 110; "left-handedness," 393; xanthochroism, 126, 306
Parrot, Burrowing (*Strigops*), 162
Parrot, Thick-billed (*Rhynchopsitta pachyrhyncha*), 301, 424
Parrot fever (psittacosis), 406, 407
Parthenogenesis, 99
Partridge, Chuckar, 260
Partridge, European (*Perdix perdix*): age, 142; cycles, 258; exotic, 260; flight, 288; heart, 87; protection, 411; respiration, 87
Parulidae, 164, 166, 291; calls, 153; radiation, 166
Pathways of spread, 175–177
Pattern in nature, 230
Patterned sound, 319
Passerines (Passeriformes), 32, 33, 38, 46, 62, 78, 166; age, 139–140, 141; bathing, 410; eggs, 249, 370; flight, 287; flocking, 240; frequency, 336; incubation, 109, 110, 371; monogamy, 348; origin, 196; parasites, 405; Pleistocene, 152; roosting, 208; sounds, 321; survival, 93; weight, 90
Peafowl (*Pavo cristata*), 42, 132, 450
Peck order, 221, 231, 233
Pecten, 309
Pectoral girdle, 55, 56
Pelican (*Pelecanus*), 16, 47, 61, 79, 305, 461; age, 136; bill, 42; body temperature, 83; cooling, 88; feeding, 384; habits, 233, 241; parasites, 384; respiration, 87
Pelican, Brown (*Pelecanus occidentalis*), 83, 238, 439, 440
Pelican, White (*Pelecanus erythrorhynchos*), 64, 174, 283
Pellet analysis, 251
Pelvic girdle, 55–56
Penelope, Black (*Penelopina nigra*), 330
Penguin (Spheniscidae), 16, 35, 37, 48, 113, 155, 163; cartoon art, 472; competitors, 37; distribution, 174; egg, 107; grit, 62; incubation, 109, 110; migration, 297, 309; nesting, 222; temperature, 83; territory, 222
Penguin, Adélie (*Pygoscelis adeliae*), 92, 233, 355, 365, 384
Penguin, Emperor (*Aptenodytes forsteri*), 418
Penguin, Gentoo (*Pygoscelis papua*), 99, 233, 356
Penguin, Ringed (*Pygoscelis antarctica*), 233
Penguin, Yellow-eyed (*Megadytes antipodes*), 348, 383
Pennsylvania, 218, 343, 420, 421
Perdicidae, 152
Petrel (Hydrobatidae), 36, 354; egg, 107, 370; feeding, 385; habits, 203
Petrel, Black-capped (*Pterodroma hasitata*), 423
Petrel, Diving (Pelecanoididae), 106
Petrel, Leach (*Oceanodromo leucorhoa*), 276, 282
Pewee, Eastern (*Myiochanes virens*), 83, 312, 332
Pewee, Western (*Myiochanes richardsoni*), 337, 342
Phalarope (Phalaropodidae), 82, 283, 349, 379, 394
Pharynx, 60, 61, 65

Pheasant (Phasianidae), 19, 28; age, 141; disease, 406; exotic, 260; origin, 195; protection, 411
Pheasant, Lady Amherst (*Chrysolophus amherstiae*), 353
Pheasant, Ring-necked (*Phasianus colchicus*), 87; age, 137; display, 233, 353; flapping, 277; heart, 87; polygamy, 349; territory, 226
Phenology, 213
Phoebe, Eastern (*Sayornis phoebe*): banding, 469; habits, 189; migration, 306, 313; nest site, 430, 431; song rate, 335
Photography, 465–466
Photoperiod; *see* Day length
Phyla of Animal Kingdom, 13–14
Physiology, 81–95
Picture writing, 412, 413
Pigeon (*Columba*), 8, 16, 40; age, 144; breeds, 398; control, 449; food, 436; flight speed, 288; heart, 87; milk, 61; navigation, 307; heat, 85; respiration, 87; sperm, 96
Pigeon, Band-tailed (*Columba fasciata*), 107, 443
Pigeon, Passenger (*Columba migratoria*): age, 136; biomass, 256; colonies, 253; decoys, 450; distribution, 174; egg, 107, 209, 421; extinction, 419, 421–422; extinction threshold, 253; feeding, 256–282; migration, 305; monument, 421; nesting, 223, 227; numbers, 256; salt, 443
Pigeon, Red-billed (*Columba flavirostris*), 237, 424
Pigeon, White-crowned (*Columba leucocephala*), 424
Pigments, 123–125
Pinch period, 211–212
Pipit (*Anthus*), 183, 195, 283, 305, 330
Pipit, American (*Anthus spinoletta*), 175; *see also* Pipit, Rock
Pipit, Meadow (*Anthus pratensis*), 174, 234
Pipit, Rock (*Anthus spinoletta*), 330
Pipit, Tree (*Anthus trivialis*), 174, 330
Pitch, 335
Pitta, 193
Pituitary, 71, 72, 294
Plant distribution by birds, 446–447
Plantain-eaters (Musophagidae), 124
Plasmogyps patritus, 157
Pleisiocathartes, 157
Pleistocene, 151, 152, 155, 156, 173, 363
Pliocene, 156, 157, 173
Plover, 130, 284
Plover, Golden (*Pluvialis dominica*), 296, 297, 308
Plover, Ringed (*Charadrius hiaticula*), 233
Plumage and aquatic life, 48
Plumage names, 120–122
Plumage trade, 453
Plumage use, 416–417
Plunging, 277, 439–440
Poisons, 408
Polyandry, polygamy, 348
Poorwill (*Phalaenoptilus nuttalli*), 462
Population, 244–250; age composition, 136–138; curve, 259; cycles, 258–259; density, 253–254; limit by territory, 225; measurement, 246–247; problems, 474; reservoir, 228, 229, 257–258; total, 261
Prairie Chicken (*Tympanuchus cupido*), 35, 63, 157, 164; courtship, 349; display, 323; distribution, 187; migration, 297; moved, 260; roosting, 209; voice, 322, 323
Prairie Chicken, Attwater (*Tympanuchus cupido attwateri*), 423, 427
Pratincole (*Glareola*), 330
Predation, 130, 239, 251, 447
Predator value, 447
Premature acts, 388
Prey selection, 153
Primitive characters, 25
Priority, 31, 33
Procellariiformes, 110
Productivity, 250
Prolactin, 99
Promiscuity, 348
Properties of air, 274
Protection, 411–424; colonial birds, 416–417; early, 411–413; island birds, 417–418; large birds, 414–415; model Audubon law, 415; model hawk and owl law, 415; rare and threatened species, 424
Proventriculus, 61, 62
Ptarmigan (*Lagopus*), 157, 164; albinism, 125; distribution, 172, 183; flight, 283; flight song, 330; injuries, 409; molt, 119; plumage, 119, 158; roosting, 209; weight, 64
Ptarmigan, White-tailed (*Lagopus leucurus*), 175, 216, 261
Pteranodon, 269, 271
Pterodactyl, 8, 271
Pterosauria, 6, 7, 17, 162, 269, 271
Puffin, 44, 106
Puffin, Tufted (*Lunda cirrhata*), 107
Pygostyle, 40

Pyramid of numbers, 444
Pyrrhuloxia, 166

Quadrupedal climbing, 38
Quail, 28, 135, 195, 249
Quail, Button (*Turnix*), 348
Quail Gambel (*Lophortyx gambeli*), 63, 232
Quail, Mountain (*Orerortyx picta*), 45, 87, 171, 260
Quail, Scaled (*Callipepla squamata*), 87
Quail, Valley (*Lophortyx californica*), 45; age, 137; age ratios, 138; drinking, 92; exotic, 260; range, 174; roosting, 208; sex ratio, 146
Quebec, 421
Quetzal (*Pharomachrus mocinno*), 411

Race, 26, 32
Racial age, 163; senescence, 155-156
Radiation, adaptive, 163-165; evolutionary, 35
Radiation of families, 164, 166; Buteonidae, 164; Fringillidae, 163, 164; Strigidae, 163, 164; Tetraonidae, 163, 164; Turdidae, 164
Rail (Rallidae), 166, 200, 305, 370
Rail, King (*Rallus elegans*), 100
Rail, Laysan (*Porzanula palmeri*), 163
Rail, Wood (*Aramides*), 163
Rancho La Brea, 151, 152, 155, 156
Range, 189-197, 220; activity, 220; home, 220; kinds of, 220-223
Range and mobility, 190
Range complex, 189
Range continuity, 190
Range discontinuity, 190-191
Range size, 189-190
Rare and threatened species, 423-427
Raven (*Corvus corax*), 26, 63, 164, 461; adaptations, 188; age, 135, 137, 143; albinism, 125; distribution, 183, 227; flight, 283; mutation, 241; range, 190; temperature, 83; totem art, 413
Recent, 151, 152, 156, 157
Recognition marks, 130-131
Recording instruments, 467
Redbreast; *see* Robin, British
Redpoll (*Acanthis flammea*), 262, 305
Redstart, American (*Setophaga ruticilla*), 42, 142, 202; display, 131; plumage, 122; protection of young, 384; song rate, 334
Redstart, European (*Phaenicurus phaenicurus*), 136, 216
Refractory period, 99, 295
Relation of physiology and ecology, 49
Relation of structure and function, 34
Relationships, 13-23, 25
Relative abundance of species, 260-261
Releasers, 149, 352, 380
Relict species, 190
Renesting, 370-371
Repetition of song, 335
Reproduction and isolation, 151
Reproductive system, 70-71, 96-99
Reptiles, flying, 269-271
Respiration rate, 86-88
Rhamphorhyncus, 269
Rhea (Rheidae), 110, 297
Rhinoceros Bird; *see* Ox-pecker
Rhythm: breeding, 98-99; musical, 338, 342
Rhythms, population, 258-259
Richmondeninae, 153, 166, 195, 292
Riparian avifauna, 175
Road-runner (*Geococcyz californianus*), 243, 284, 371
Robin, American (*Turdus migratorius*), 46, 60, 139, 347, 349, 386, 431; abundance, 261; adaptation, 187; age, 136, 142; age ratios, 138; albinism, 125; bathing, 410; call, 328; distribution, 179; egg, 249; evening song, 213; feathers, 118; flapping, 277; flight muscles, 279; food, 134; gliding, 280; habits, 189; injuries, 409; intoxication, 408; life expectancy, 135, migration, 238, 298, 305; nest sites, 430; nestling, 386; nests, 363, 373; protection, 384; respiration, 87; singing at eclipse, 33; song, 337; song cessation, 332; temperature, 82, 83; territory, 226; water, 429; weight, 273; wing, 282; wing load, 276; winter feeding, 428
Robin, British (*Erithacus rubecula*), 436; age, 136, 137; age ratios, 138; habits, 224; life expectancy, 139; medical nostrums, 453; sex recognition, 348; territory, 229
Rodriguez, extinct birds of, 423
Roller (*Coracias garrulus*), 193, 356
Rook (*Corvus frugilegus*), 136, 176, 300, 411
Roosting, 51, 57, 207-209, 379, 462
Ruff (*Philomachus pugnax*), 131, 349
Rules of nomenclature, 30-31
Ruling reptiles, 6, 7, 16

Salivary glands, 61, 363
Salt, 92, 443
Salt lick: birds attracted by, 92; chemical composition, 92
Sample areas, 469

Sandpiper, 283, 409
Sandpiper, Spotted (*Actitis macularia*), 283
Sapsucker (*Sphyrapicus*), 61, 438
Sarcoramphus kernensis, 156, 157
Saturation point, 211
Saunders' diagrams, 338
Saurischia, 7
Scales (foot), 46, 47
Scales, musical, 341–342
Scansorial, 41
Scientific method, 456–457, 459
Scientific nomenclature, 29–32
Sclerotic ring, 11, 19, 76
Seasonal influences, 212–214
Secretary Bird (*Sagittarius serpentarius*), 44, 357
Selection of mates, 350
Sense organs, 72–80
Sequestration notes, 328
Sex characters, inheritance of, 393–394
Sex counts, 246
Sex determination, 394–395
Sex dominance, 355
Sex ratios, 146–147, 235–236, 349, 395
Sex recognition, 131, 347–348
Seymouria, 7
Shearwater (*Puffinus*), 21, 203, 292, 385
Shearwater, Manx (*Puffinus puffinus*), 385, 386
Shearwater, Sooty (*Puffinus griseus*), 376, 385, 386
Shearwater, Wedge-tailed (*Puffinus pacificus*), 159
Shelduck (*Tadorna tadorna*), 301
Shelters and roosts, 207–209
Shorebirds (Charadridae), 46, 47, 48; color, 129, 130; egg color, 103; egg shape, 101; egg size, 101, 104; eggs, 249; flight speed, 287; flocks, 238; migration, 305, 306, 474; mutualism, 240; roosting, 209
Shrike (Laniidae), 195; eggs, 370; food, 441, 443
Shrike, Loggerhead (*Lanius ludovicianus*), 223, 444, 445
Shrike, Northern (*Lanius excubitor*), 239, 303
Siblings, 25
Singing: monotony threshold, 334; responsive, 342–345
Singing hours, 333
Singing season length, 331–333
Siskin, Pine (*Spinus spinus*), 305, 443
Site tenacity, 237, 253
Size and heat production, 84
Skeleton, 20, 49–57, 273
Skimmer, Black (*Rynchops nigra*), 42, 54, 193, 283, 440, 441
Skua (*Catharacta*), 241
Skull, 20, 52–54, 139–140
Skylark (*Alauda arvensis*), 126, 180, 283, 300, 329
Slave birds, 450
Sleep, 93; *see also* Roosting
Snakes, 7
Snipe (*Capella*), 126, 130, 283, 326, 330
Snipe, Painted (*Rostratula*), 348
"Snowshoes," 28, 35
Soaring, 281
Social hierarchy, 230
Social parasitism, 234–238
Social relations, 231–243
Social releasers, 149
Social stimulation and breeding, 361
Song and season, 331
Song and territory, 228
Song flight, 281, 283, 352
Song of female, 330–331
Song physics, 335–337
Song rate, 334
Song sequence, 332
Song structure, 335–345
Songs, methods of describing, 338–341
Songs and calls, function of, 326–329
Sounds, instrumental, 322–323
South Carolina, 199
Sparrow, Belding (*Passerculus beldingi*), 166
Sparrow, Black-chinned (*Spizella atrogularis*), 166
Sparrow, Brewer (*Spizella breweri*), 160, 166
Sparrow, Chipping (*Spizella passerina*), 166, 431; abundance, 261; adaptation, 187; eggs, 370; morning song, 214; nests, 363; parasites, 401; respiration, 87; song rate, 334, 335; temperature, 83
Sparrow, Clay-colored (*Spizella pallida*), 166, 334, 335
Sparrow, Desert (*Amphispiza bilineata*), 164, 166
Sparrow, European Tree (*Passer montanus*), 260
Sparrow, Field (*Spizella pusilla*): brooding, 382; ecology, 201, 206; eggs, 370; feeding young, 375; growth, 377, 378; music, 340; numbers, 255
Sparrow, Fox (*Melospiza iliaca*), 28, 166, 185, 318
Sparrow, Gambel; *see* Sparrow, White-crowned

Sparrow, Grasshopper (*Ammodramus savannarum*), 166, 201, 329, 337
Sparrow, Harris (*Zonotrichia querula*), 318
Sparrow, Hedge (*Prunella modularis*), 372, 453
Sparrow, Henslow (*Passerherbulus henslowii*), 201
Sparrow, House (*Passer domesticus*), 42, 63, 158, 428; abundance, 261; albinism, 125, 396; albinism and flock continuity, 240; bathing, 410; body variation, 94; color, 125; control, 431, 449; disease, 406, 407; egg, 107; energy balance, 85; energy intake, 94; flight, 288; flocking, 238; heart, 87; heat, 84; hovering, 336; nesting, 223, 360, 362; numbers, 261; plumage, 122, 123; respiration, 87; spread, 188, 259-260; survival, 94; weight, 64; wing, 282; wing load, 276
Sparrow, Lark (*Chondestes grammacus*), 176, 201
Sparrow, Lincoln (*Melospiza lincolnii*), 28, 340
Sparrow, Rock (*Aimophila ruficeps*), 176
Sparrow, Savannah (*Passerculus sandwichensis*), 166, 200, 201, 208, 214, 255, 329
Sparrow, Seaside (*Aimospiza maritima*), 190, 424
Sparrow, Song (*Melospiza melodia*), 28, 164, 349; abundance, 261; adaptation, 187; age, 136, 137; anting, 242; behavior, 381; call, 328; color, 186, ecology, 201, 210; flight, 283; flocking, 238; light, 214; migration, 300; minimum area, 252; morning song, 214; mortality, 388; music, 340, 341, 342, 343, 344; nest box, 430; numbers, 254, 255; range, 190; roosting, 208; sex ratio, 146; sex recognition, 348; song, 336, 337; song rate, 335; temperature, 82, 83; territory, 226, 229; water, 429
Sparrow, Swamp (*Melospiza georgiana*), 28, 111, 164, 201, 283
Sparrow, Tree (*Spisella arborea*), 94, 238, 261, 318
Sparrow, Vesper (*Pooecetes gramineus*), abundance, 261; bathing, 410, 411; ecology, 200; habits, 153; radiation, 164, 166; territory, 226
Sparrow, White-crowned (*Zonotrichia leucophrys*), 94, 349; hours of singing, 333; music, 340, 342; nesting, 360; shelter, 216
Sparrow, White-throated (*Zonotrichia albicollis*), 94; food, 442; habits, 224; music, 340; roots, 208; song, 338; wintering, 317, 318
Specialization and racial age, 163
Species, 25–26
Species association, 232–233
Species groups, 158
Spermatozoa, 71, 96–97, 99, 256
Spermatozoa viability, 99
Sphenodon, 6, 7, 23
Spizella, 166
Spoonbill (*Ajaja*), 79, 424, 425
Spread, accidental, 177
Spreadways, 175–177
Squirrel, Flying, 271
Starling (*Sturnus vulgaris*), 16, 354; abundance, 253, 261; age, 136; age ratios, 138; banding, 469; caged, 450; control, 449; flapping rate, 277; flight, 283; flight speed, 287; flocking, 238, 239; hearing, 335, 336; inheritance, 397; life expectancy, 139; migration, 300, 305; nesting, 223; respiration, 87; roosting, 213; sex ratio, 146; song, 337; spread, 188, 259-260; weight, 64
Starvation, 90, 93–94
Stem reptiles, 6, 7
Stimulus reception, 75
Stomach, 60, 61, 64
Stork (Ciconiidae), 152, 305, 321, 405, 406, 469
Streamline, 21
Structural adaptations, 37–48
Studies, kinds of, 472–474
Substitution ability, 186–187
Succession and habitat, 199–205
Sunbird (Nectariniidae), 61, 193
Survival and energy, 93–95
Survival values, evolutionary, 149, 150, 156
Swallow (Hirundinidae), 76, 195, 368, 431; altitude of migration, 304; feeding, 282; flight, 283; growth, 386; migration, 305; roosts, 207; visual distance, 465
Swallow, Bank (*Riparia riparia*), 36; arrival, 313; habitat, 183; flapping rate, 277; flight, 283, 284; flight gait, 278; nest, 364, 365
Swallow, Barn (*Hirundo rustica*), 41, 63; abundance, 261; albinism, 125, 386; arrival, 313; flapping rate, 277; flight, 286, 287; habits, 189; nesting, 223; nest sites, 430; nests, 363, 364; wing load, 276
Swallow, Cliff (*Petrochelidon pyrrhonota*): arrival, 313, 314, 315; flapping, 277; flight, 283, 287; habitat, 183; hab-

Swallow, Cliff—*continued*
its, 189; migration departure, 312; needs, 171; nest sites, 430; nests, 363, 364; roosting, 208
Swallow, Rough-winged (*Stelgidopteryx ruficollis*), 277, 287, 313
Swallow, Tree (*Tridoprocne bicolor*): arrival, 313; flapping, 277; flight, 283, 287; habits, 189; nest box, 430; nest parasites, 405; wing load, 276
Swallow, Violet-green (*Tachycineta thalassina*), 189, 254, 430
Swallow, Wood (Artamidae), 116
Swan (Cygninaë): color, 125; domestication, 452; feeding, 441; flocking, 237; pairing, 348; parasites, 405
Swan, Black (*Cygnus atratus*), 106
Swan, Mute (*Cygnus olor*), 106, 260
Swan, Trumpeter (*Cygnus buccinator*), 63, 321–322, 424, 425
Swan, Whistling (*Cygnus columbianus*), 118, 267, 288, 321–322, 379
Swift (Apodidae), 38, 39, 61, 76; flight, 277, 283; growth, 386; migration, 305; parasites, 405; wing action, 277
Swift (*Collocalia*), 61
Swift (*Micropus caffer*), 369
Swift, Chimney (*Chaetura pelagica*), 21, 41, 47; albinism, 125; banding, 470; feeding, 282; flapping, 277; habits, 189; hours aloft, 191; nest sites, 430; roosting, 207; vertical flight, 281; wing action, 279; wing shape, 279
Swift, White-throated (*Aëronautus saxatalis*), 170
Sylvidae, 195
Symbiosis, 240
Sympatric species, 26, 191–192
Syrinx, 65, 320–321, 330
Systema Naturae, 30, 31, 33

Tail adaptations, 39–42; length, 39, 40, 167–168
Tanager, Scarlet (*Piranga olivacea*), 200
Tanagers (Thraupidae), 193, 195, 292, 305
Taxonomy, 24–32
Teal, Blue-winged (*Anas discors*), 273, 283, 297, 315
Teal, European (*Anas crecca*), 469
Teal, Laysan (*Anas wyvilliana*), 261
Teeth, 12, 19, 20
Temperature: body, 16, 18, 75, 82–83; thermo-neutral, 89
Temperature and distribution, 174
Temperature and metabolic rate, 86
Temperature and survival, 93–94
Tennessee, 213, 360, 422
Teratornis, 151, 152, 156, 157
Tern (Sterninae), 166, 431; eggs, 370; feeding, 282; habits, 241; hatching, 376; islands, 417; nesting, 361; parasites, 404
Tern, Aleutian (*Sterna aleutica*), 424
Tern, Arctic (*Sterna paradisaea*), 41, 310, 311, 317–318, 373
Tern, Caspian (*Hydroprogne caspia*), 262
Tern, Common (*Sterna hirundo*), 227, 237, 253, 263, 288, 348, 355
Tern, Roseate (*Sterna dougalli*), 263, 424
Tern, Sooty (*Sterna fuscata*), 358; *see also* Wide-awake
Territorial relations: behavior, 474; boundaries, 226, 228; defense, 226–227; function, 225; polygamous species, 226; population limitation, 228–229; song, 228
Territory, 210–229; colonial, 223; communal, 221; definition, 220; history, 219–220; kinds, 220–223; selection, 225–226; size, 228; winter, 221, 224
Testes, 71, 96–97, 99
Texas, 41, 159, 259, 307, 318, 334, 412, 421, 442
Thecodonts, 6, 7, 8
Thermals, 280, 281
Thrasher, 354
Thrasher, Brown (*Toxostoma rufum*), 100, 185, 243
Thrush (Turdidae), 195, 368; distribution, 183; migration, 305; music, 340, 344; singing, 334; winter feeding, 428
Thrush, Gray-cheeked (*Hylocichla minima*), 297
Thrush, Hermit (*Hylocichla guttata*), 164, 332, 337, 340, 343
Thrush, Song (*Turdus ericetorum*): age, 136; age ratios, 138; food, 436; incubation, 372; life expectancy, 139; mortality, 139
Thrush, Wood (*Hylocichla mustelina*), 164, 200, 254, 339
Thunderbird, 413
Time-depth ratio, 440
Time of singing, 331–335
Tinamou (Tinamidae), 102, 195
Tit (Paridae), 132, 158
Tit, Bearded (*Panurus biarmicus*), 176
Tit, Blue (*Parus caeruleus*): age, 136; distribution, 176; ecology, 230; eggs, 370; food, 436; young, 376
Tit, Great (*Parus major*): age, 136; eggs, 370; food, 436; growth, 377; incubation, 371; young, 376

Tit, Marsh (*Parus palustris*), 136, 372
Titmouse, correct form of plural, 232
Titmouse, Tufted (*Parus bicolor*), 45; abundance, 254, 261; bathing, 410; crest, 44; distribution, 176; habits, 232; nest box, 430; weight, 185
Tolerance of change, 186–189
Tongue, 55, 60
Tooth, egg, 375
Topographic influences, 183–185
Totem art, 413
Toucan (Rhamphastidae), 44, 149–150, 195
Toucanet, Emerald (*Aulacorhynchus prasinus*), 293, 301
Towhee (*Pipilo*), 79
Towhee, Red-eyed (*Pipilo erythrophthalmus*), 146; ecology, 201; feathers, 120; music, 338, 342, 344; song season, 332
Trachea, 61, 65
Tradition, 158, 317
Trapping for banding, 470
Trogon (Trogonidae), 171, 183, 193
Tropic-bird (Phaëthontidae), 292
Turacin, 124
Turacoverdin, 124
Turkey (Meleagrididae), 28, 152, 195
Turkey (*Meleagris gallapavo*), 16, 28, 46, 57, 151, 379, 380, 421; broods, 382; display, 132; domestication, 451; drinking, 92; eggs, 107, 249, 370; habits, 233; heart, 87; heredity, 393, 394; laying time, 108; migration, 297; parthenogenesis, 99; respiration, 87; survival time, 94
Turkey (*Meleagris tridens*), 151
Turnicidae, 110
Turnstone (*Arenaria interpres*), 298
Turtle, 7
Tytonidae, Pleistocene, 152

Ultra-violet penetration in North, 90
Umbrella-bird (*Cephaloperus glabricollis*), 353
Ungulate niche, 36
Uphill planters, 446
Urogenital system, 62, 69, 70, 97, 98
Utah, 202

Variability of body parts, 94
Variability of domestic birds, 161
Variation gradient (cline), 159–160
Variations, 157–163; adaptive, 149, 150; continuous and discontinuous, 158–161; factors affecting, 34–37; non-adaptive, 149, 150
Variations and survival relations, 34–35
Veery (*Hylocichla fuscescens*), 164, 444
Vegetation influences, 182
Vegetation types, 180
Vegetation zones, 203–204
Vertebrata, 14–15
Viability of sperm, 99, 356
Vireo (Vireonidae), 193, 354; feeding, 254; migration, 291, 305; singing on nest, 329
Vireo, Bell (*Vireo belli*), 332
Vireo, Blue-headed (*Vireo solitarius*), 254, 256
Vireo, Red-eyed (*Vireo olivaceus*): needs, 206; nest, 368; noon-time song, 333; numbers, 254; song rate, 334, 335
Vireo, Warbling (*Vireo gilvus*), 333
Vireo, Yellow-green (*Vireo flavoviridis*), 292
Vireo, Yellow-throated (*Vireo flavifrons*), 332, 333
Virginia, 420, 422
Vision, 42, 75–78; binocular, 76
Visual acuity of birds, 76
Visual circle, 76–77
Visual distance, 465
Vitamins, 90, 442
Volume of habitat, 207
Vulnerability, 251
Vultur gryphus, 157
Vulture, Black (*Coragyps atratus*), 63, 155, 156, 165, 280–281, 386, 461
Vulture, Turkey (*Cathartes aura*), 155, 156, 165, 461; feeding, 240; sinking speed, 280–281; smell, 474; temperature, 83; visual distance, 465; weight, 64; wing load, 267, 282
Vultures, 16, 46, 61, 156, 157, 272, 276; antisepsis, 407; migration, 305; soaring, 280; wind relations, 218

Wagtail, Gray (*Motacilla cinerea*), 176
Wagtail, Yellow (*Motacilla flava*), 229
Warbler (Paruliade), 42, 165, 166, 193, 195, 209, 368; age, 135; banding, 470; brooding, 383; ecology, 202; feeding, 254, 282, 438; frequency, 336; hearing, 335; migration, 305; music, 340
Warbler, Bachman (*Vermivora bachmanii*), 190, 202
Warbler, Black and White (*Mniotilta varia*), 202, 299, 332, 336
Warbler, Black-throated Blue (*Dendroica caerulescens*), 202
Warbler, Black-throated Green (*Dendroica virens*), 175, 202

Warbler, Blackpoll (*Dendroica striata*), 299, 337
Warbler, Blue-winged and Golden-winged hybrids, 392–393
Warbler, Canada (*Wilsonia canadensis*), 202
Warbler, Chestnut-sided (*Dendroica pensylvanica*), 202
Warbler, Colima (*Vermivora crissalis*), 424
Warbler, Golden-cheeked (*Dendroica chrysoparia*), 190, 261, 424
Warbler, Hooded (*Wilsonia citrina*), 126
Warbler, Kirtland (*Dendroica kirtlandii*), 165, 180, 188, 190, 246, 261, 368, 424
Warbler, Magnolia (*Dendroica magnolia*), 83, 202
Warbler, Myrtle (*Dendroica coronata*), 42, 135, 164, 166, 175
Warbler, Nashville (*Vermivora ruficapilla*), 202
Warbler, Orange-crowned (*Vermivora celata*), 312
Warbler, Pileolated (*Wilsonia pusilla*), 312
Warbler, Pine (*Dendroica pinus*), 135, 185
Warbler, Prairie (*Dendroica discors*), 340
Warbler, Prothonotary (*Protonotaria citrea*), 334, 335, 360, 364, 368, 375
Warbler, Reed (*Arocephallus scirpaceus*), 229
Warbler, Sutton (*Dendroica potomac*), 424
Warbler, Tolmie (*Oporornis tolmiei*), 312
Warbler, Townsend (*Dendroica townsendi*), 166
Warbler, Willow (*Phylloscopus trochilus*), 229
Warbler, Yellow (*Dendroica petechia*), 166; abundance, 261; adaptation, 187; age, 135; ecology, 200; nesting, 368; song, 332
Warbler, Yellow-throated (*Dendroica dominica*), 332
Warm-blood, 17, 170
Warning calls, 328
Washington, 147, 171, 262, 263, 368
Water and energy entrapment, 199
Water needs, 92, 474; sources, 92
Water-thrush, Louisiana (*Seiurus motacilla*) 202
Water walking, 286
Waterfowl (Anseriformes), 47, 465; age, 141, 143, 144, 145; banding, 470; counts, 246; drinking, 92; feeding, 441; lead poisoning, 408; migration, 300; oil gland, 116; parasitism, 234; protection, 411; sickness, 407
Waxwing (Bombycillidae), 195, 238, 305, 428
Waxwing, Bohemian (*Bombycilla garrula*), 239, 283, 303, 429
Waxwing, Cedar (*Bombycilla cedrorum*), 261, 283, 336, 408, 438, 446
Weaver, Masked (*Ploceus cucullatus*), 437
Weaver, Red-billed (*Quelea quelea*), 363, 437
Weaver-finch (Ploceidae), 223, 234, 237, 349, 354, 364, 368
Weaver-finch (*Vidua macroura*), 236
Weight: body parts, 64, food ratio, 436–437; hatching, 376–379; variations, 90–91
Weight and Bergmann Rule, 185
Whip-poor-will (*Caprimulgus vociferus*), 103, 305, 333, 462
Whitethroat (*Sylvia communis*), 330
Wide-awake (*Sterna fuscata*), 292, 358
Widgeon, European (*Mareca penelope*), 30, 315
Willet (*Catoptrophorus semipalmatus*), 39
Wilson Ornithological Society, 416
Wind relations, 217–218, 300
Wing flapping rate, 277–278
Wing flashing, 243
Wing loading, 275–276
Wing ornamentation, 39
Winter food, 427–429, 442
Wisconsin, 126, 187, 224, 421, 422, 430
Woodcock (*Philohela minor*), 48, 166, 462; counts, 247; flight, 283, 286, 353; flight speed, 288; hatching, 376; limitation, 174; sounds, 324, 325; wing load, 276
Woodhewer (Dendocolaptidae), 41, 321
Woodpecker (Picidae), 41, 42, 47, 60, 61, 165, 354, 368; bark beetles, 444; color, 125, 128; egg, 102; feathers, 121; growth, 386; hatching, 376; hybrids, 398; incubation, 110; migration, 305; nesting, 364; Pleistocene, 152; winter feeding, 428
Woodpecker, Downy (*Dendrocopus pubescens*), 26, 439, 440; abundance, 254, 261; biomass, 256; blight, 446; distribution, 179, 192, 194; ecology, 210; flocks, 238; nest box, 430; respiration, 87; temperature, 83; weight, 185
Woodpecker, Golden-fronted (*Centurus aurifrons*), 430
Woodpecker, Greater Spotted (*Dendrocopus major*), 128, 131

Woodpecker, Hairy (*Dendrocopus villosus*), 26; biomass, 256; distribution, 192, 194; feeding, 438; nest box, 430; respiration, 87; weight, 185
Woodpecker, Ivory-billed (*Campephilus principalis*), 165, 188, 424, 427
Woodpecker, Pileated (*Ceophloeus pileatus*), 182, 283
Woodpecker, Red-bellied (*Centurus carolinus*), 176
Woodpecker, Red-headed (*Melanerpes erythrocephalus*), 170, 182, 430, 443
Woodpecker, Three-toed (*Picoides*), 182
Wren (Troglodytidae), 103, 163, 195, 213, 305, 340, 368
Wren, Bewick (*Thryomanes bewickii*), 185, 309, 430
Wren, Canyon (*Catherpes mexicanus*), 183
Wren, Carolina (*Thryothorus ludovicianus*), 174, 176, 336, 430
Wren, House (*Troglodytes aedon*), 349; egg, 106; feathers, 121; feeding, 385; habits, 189; incubation, 371; insecticides, 446; nest box, 430; nest parasites, 430; nesting, 362; population, 244; respiration, 87
Wren, Marsh (*Telmatodytes palustris*), 121, 166, 283
Wren, St. Kilda (*Troglodytes troglodytes*), 229, 261
Wren, Winter (*Troglodytes troglodytes*), 334
Wren-tit (*Chamaea fasciata*), 168, 229
Whydah, Paradise (*Steganura orientalis*), 42
Wyoming, 215

Xanthochroism, 126

Yellowlegs (*Totanus*), 19, 298
Yellowthroat (*Geothlypis trichas*), 135, 164, 166, 185, 202

Zoogeographic factors of distribution, 169
Zoogeographic laws of distribution, 171–173
Zoogeographic Realms, 177–178
Zone, subvegetation, 36
Zugunruhe, 295
Zygodactyly, 48